EFFECTS OF DAMAGE-INDUCED AND DEVELOPMENTAL CHANGES OF WHITE BIRCH (*BETULA PAPYRIFERA* MARSH.) ON POPULATIONS OF BIRCH CASEBEARER (*COLEOPHORA SERRATELLA* L.) (LEPIDOPTERA: COLEOPHORIDAE)

MICHELE D. PIERCEY-NORMORE

Effects of damage-induced and developmental changes of white birch (*Betula papyrifera* Marsh.) on populations of birch casebearer (*Coleophora serratella* L.) (Lepidoptera: Coleophoridae).

BY

© Michele D. Piercey-Normore

A thesis submitted to the School of Graduate Studies in partial fulfillment of the requirements for the degree of Master of Science

Department of Biology
Memorial University of Newfoundland

June 1993

St. John's Newfoundland

ISBN 0-315-96058-2

Canada

Abstract

Insects feeding on a plant may induce changes within the leaves which affect success of insects subsequently feeding on that plant. The objective of this study was to demonstrate if birch casebearer feeding on birch leaves induced changes in the tree that would deter subsequent feeding by the same insect species.

White birch trees were divided into four treatment groups of five trees each. Treatments consisted of birch leaves being severely damaged by insect feeding, lightly damaged by insect feeding, mechanically damaged with no insects present, and control with neither type of damage. Comparisons were made among treatment groups for 1) changes in the leaves, 2) population size of the birch casebearer at various times of the season, and 3) effects of damage-induced leaf changes on larval size. Damage-induced changes in the leaves were evident in nitrogen and phosphorus levels between 1991 and 1992, long-shoot length and number of buds, and bud development and leaf senescence. These changes were likely a result of nutrient depletion by insect feeding the previous year, reducing the tree's ability to compensate for losses. Population size of the birch casebearer between treatment groups changed very little throughout 1991 and 1992 suggesting that moths did not move far from the site of pupation. Positive correlation between nitrogen levels and egg density suggested that female moths might be able to distinguish between high and low leaf nitrogen levels,

though this could occur within the same tree. Since headcapsule widths of Instar II larvae did not differ significantly between treatment groups, it appeared that damage-induced changes of white birch had no measurable effect on larval size.

Leaf developmental changes, measured as water potential, water content, and fresh and dry leaf weights, were compared with seasonal changes in plant and insect life history stages. Egg hatch coincided with second leaf flush. Since eggs were laid on old leaves, it was suggested that Instar I larvae took advantage of nutrients being mobilized out of the older leaves and moving into younger leaves.

The study showed no evidence for damage-induced leaf changes affecting success of the birch casebearer. However, there was speculation that the unusual life history pattern of the birch casebearer was adapted so that Instar I and II larvae could take advantage of mobilized leaf nutrients, lower water contents, and water potentials late in the season. Instar III and IV larvae, with faster growth, could take advantage of high leaf nutrients early in the season.

Acknowledgements

I wish to thank my supervisor, Dr. D. J. Larson, for his constant encouragement and support, moral, financial, and academic, throughout the course of my research. During his sabbatical year he maintained continuous and fruitful correspondence, though often by way of pony express, and upon his return his guidance and generous advice grew, as well as the dubious criticisms. Our philosophical discussions primed my mind beyond that necessary for future studies, and enlightened my outlook on the scientific and academic world.

I am indebted to Forestry Canada for summer employment which initiated my studies, and their allocation of manpower and equipment; to Elizabeth Pike in the laboratory who endured my questions and untimely mistakes; to Dave Strong who offered his time and assistance in collecting insect laden twigs; to Dick Rowe who both helped and organized help for my work; and to Dr. Wade Bowers and Dr. Art Raske who aided in experimental design and offered much appreciated advice while my supervisor was away on sabbatical. Many thanks to Dr. John Hudak who sowed the seed for my Master's project.

I am grateful to Dr. Murray Colbo who granted me free access to his lab and equipment; to Dr. Roger Lee who survived a summer without his pressure bomb; and to Dr. David Innes who offered helpful advice.

Financial support was provided partially by a provincial government scholarship "Special Scholarship for Studies in the Sciences Related to Resource Development", as well as a Graduate Fellowship award.

Lastly, I offer my appreciation to Jerry Browne who supported my afflictions for potato chips and smoky jasmine incense throughout the two years; and to Jason and Steven, my two sons who encouraged my happiness, and heightened my adrenalin levels on a regular basis.

Table of Contents

List of Tables

List of Figures

Page

I. Introduction

I.A: Damage-Induced Plant Changes:

Insects feeding on plants may elicit changes within their host plants that may, or may not, have a subsequent effect on the insect. These plant changes are a consequence of feeding damage caused by herbivores and are referred to as 'damage-induced changes'.

Damage-induced changes in plants have been widely studied (Levin, 1976; Ruohomaki et al, 1992) and they are considered either passive or active. Passive plant changes involve changes within the plant as a physical consequence of damage such as depletion of nutrients or photosynthetic area as a result of insect consumption of leaf tissue. Active changes involve physiological or anatomical changes within the plant as a result of earlier herbivore damage to plant tissues. Examples of damage-induced plant changes include alterations in anatomical structures like thorns or resin ducts, production of hormone-like substances that affect herbivore development, and production of secondary products that reduce plant palatability (Levin, 1976). Active damage-induced

changes made by the plant are referred to as damage-induced responses.

In studies of damage-induced plant changes caused by herbivory, emphasis has been placed on the production of plant compounds which ward off herbivores (active plant changes) as opposed to the absence of compounds required for growth of plant and insect (passive plant changes) such as water content and mineral nutrients (Haukioja et al, 1991). Some studies have concentrated on changes plant damage causes within the plants (Schultz and Baldwin, 1982), whereas others have examined the effects of these plant changes on subsequent herbivores (Bryant et al, 1991; Faeth, 1986), or on both changes within the plant and their subsequent effects on herbivores (Fowler and Lawton, 1985; Hartley and Lawton, 1987). Plant response to artificial damage has also been studied (Baldwin, 1990). Artificial damage may not resemble herbivore damage. The level of artificial damage applied may be greater or less than damage inflicted by herbivores; bacteria or fungi associated with insect damage may not be present in artificially damaged leaves; and plant changes which may be triggered by chemicals or hormones associated with herbivores would not be present in artificially damaged leaves.

Consequences of induced changes for herbivores depend upon which herbivore life stage is affected by the change, as well

as the duration of the change (Haukioja, 1990). Two types of damage-induced responses (active plant changes) occur (Haukioja, 1990). The rapid induced response (RIR) involves a response of the plant to insect damage, and this response is experienced by the same insect generation that inflicted the damage, and usually within the same growing season. For example, Haukioja and Niemela (1977) reported that larvae of the autumnal moth, Oporinia autumnata (Bkh.), attained a lower final weight when fed birch leaves that had been torn two days earlier than those larvae which were fed control leaves. A delayed induced response (DIR) has been applied to a plant response to damage inflicted by herbivores of an earlier generation and which, for univoltine species, usually occurs in the following season. For example, larval weights, growth and survival rates of the pine beauty moth, (Panolis flammea (D&S)) were lower on trees which had been defoliated the previous year than on trees not defoliated the year before (Leather et al, 1987).

Rapid induced responses function to stabilize insect populations. A rapid induced response occurs quickly, but it is also rapidly relaxed, and as a result there is a controlled oscillation of insect populations with time. As the population increases sufficiently to induce the rapid response of the tree to such a degree that the entire tree is responding, herbivore populations will begin to decline. As

the population decreases the plant's rapid response relaxes. Delayed induced responses function to de-stabilize insect populations. A delayed induced response takes a longer time to be induced, but it lasts longer, from one to four years in some plants (Haukioja, 1982). The delayed response acts to suppress the insect population, and keep it suppressed. Similarly, passive changes such as the depletion of nutrients could affect the herbivore population that caused the depletion through feeding on the tissue, or it could affect later generations by reducing the amount of stored plant reserves for the following season.

Seasonal changes associated with leaf development complicate effects of damage-induced plant changes. Seasonal changes in leaf characteristics have been well documented. Nitrogen, phosphorus, moisture levels, and palatability of birch leaves decrease throughout the growing season (Haukioja et al, 1978; Bryant et al, 1991), whereas phenolics, leaf toughness, and dry weight increase (Haukioja et al, 1978; Schultz et al, 1982).

I.B: Effects of Damage-Induced Plant Changes:

High levels of insect feeding reduce the quality of the food plant, which in turn reduces insect populations and the amount of subsequent feeding (Haukioja and Hakala, 1975). It has been shown that plant phenolics, produced when damage

occurs (Wratten et al, 1984), may increase the amount of nutritionally empty bulk food passing through the insect gut, and thus prolong larval development (Coley, 1983), or they may act to reduce the availability of nitrogen by combining with it, similarly prolonging larval development and reducing pupal weights (Haukioja and Niemela, 1977). Alternatively, the lack of required nutrients in the insect's food plant might deter feeding by the insect (Haukioja et al, 1991).

Survival of leaf-feeding insect larvae may be directly or indirectly dependent on the water status of leaves. Severe leaf water stress could have a direct impact on larval survival through dehydration, or an indirect impact by affecting larval growth by rendering nitrogen and phosphorus unavailable to the insect (Scriber, 1977), increasing the amount of cellulose/lignin which is indigestible, or causing premature senescence (Kozlowski et al, 1991).

Changes in moisture content can change plant nitrogen quantitatively (Mattson, 1980). White (1976) suggested that plant nutrients can be diluted, requiring herbivores to pass vast amounts of food through their alimentary tracts in order to obtain sufficient nutrition. Occasionally, when changes in the environment produce changes in plant moisture content that make the plant become a more nutritious food, herbivores flourish (White, 1976). For example, moderate water stress may increase leaf nitrogen levels, thereby decreasing the

amount of bulk food an insect must pass through its gut to meet nutritional need. This would decrease competition between individuals for food, shorten the time for each larval stage, and increase fecundity.

Nitrogen varies both quantitatively and qualitatively between different plant parts and influences their nutritional value as a food source. Qualitative variation is the more important for the consumer, and is much greater than the quantitative variation (Mattson, 1980). Generally, nitrogen occurs in two forms, protein and non-protein. Young, moisture-rich tissues contain larger amounts of nitrogen than mature tissues, except in senescent tissues where proteins are hydrolyzed. Young tissues are rich in all amino acids, soluble proteins, and nitrogen-based secondary compounds, whereas older tissues usually contain structural or insoluble proteins (Mattson, 1980). In many plants, including Acer, leaf nitrogen content is highest in the early season, fully expanded leaves and then declines until senescence when it drops dramatically. However, nitrogen content of Acer leaves is increased the last few days before abscission, and then is decreased dramatically (Plaisted, 1958). As water content in plant tissues decreases, nitrogen levels gradually increase, but as moisture loss intensifies, nitrogen decreases (Mattson, 1980).

Damage-induced changes in birch trees have been studied in

Finland (Haukioja and Niemela, 1977), Alaska (Bryant et al, 1987), the United Kingdom (Fowler and MacGarvin, 1986), and in the continental United States (Bergelson et al, 1986). Various workers (Haukioja and Niemela, 1977; Leather et al, 1987; and Gibberd et al, 1988) found insect defoliation of birch leaves induced changes in leaves which negatively affected larval growth. Other workers found no effect of induced plant resistance on insect performance (Myers and Williams, 1987; Bergelson and Lawton, 1988).

I.C: Host Plant Life History:

White birch, Betula papyrifera Marsh., is a broad-leaf, deciduous, monoecious tree. Growth is evident in crown expansion, which is, in turn, a function of the growth of long shoots. Long shoots emerge from the distal, pseudoterminal buds, and one or two immediately below it, on the long shoots of the previous year's growth (MacDonald and Mothersill, 1983). All proximal spurs and buds are referred to as short shoots. At bud break, in June, the first leaves to expand include two or three early leaves on the long shoot buds, as well as those on short shoots. After expansion of the first leaves there is a pause in growth. Following this quiescent stage internode extension on the long shoots occurs at a faster pace, and with it the expansion of the younger leaves. The expansion of these younger leaves is referred to as the

'second leaf flush' (July/August). New leaf development occurs into September as the older leaves begin to develop characteristic yellow/brown patches of leaf senescence. Male flower growth is induced before budburst in spring, and female in late June to early July. Seeds ripen from July to October (Perala and Alm, 1990). While nitrogen is the second most limiting element for birch, phosphorus is the first, and is required for root development (Perala and Alm, 1990).

I.D: Herbivore Life Cycle:

The birch casebearer, Coleophora serratella L., is a univoltine moth. It has four larval instars in Newfoundland (five instars in Quebec and Ontario), and is peculiar in that it overwinters as instar II (Cochran, 1970). The instar II larvae molt to instar III, and crawl from their overwintering sites in branch axils to the buds to begin feeding as birch buds turn green and leaves begin to open in early spring. By mid-June they have molted to instar IV, and have cut a new case from the upper and lower epidermis, usually from the base of a leaf. The case encloses the larva and is carried with it from Instar II until pupation. They then exit the old cases, and continue feeding from the new case of instar IV. The larva pupates within this case, which it attaches firmly to the upper surface of a leaf. Adult moths emerge mid July to early August, mate, and lay eggs. Eggs are laid on the

undersurface of a leaf, near the major veins. The larvae hatch and chew their way through the lower epidermis into the leaf where they feed on the upper and lower mesophyll layers. Instar I larvae have no cases and act as true leafminers in that they feed on and remain entirely inside the leaf epidermes. An instar I larva molts to instar II in mid September, and cuts a case from the epidermes between which it fed as instar I. Instar II larvae are then able to move out onto the leaf. Feeding resumes, as the larva can now move from leaf to leaf carrying its case with it, until conditions require that the larva go into diapause. Larvae then crawl to branch, twig, spur, or bud axils to overwinter as the leaves fall from the tree (Cochran, 1970).

I.E: Economic Importance of Study:

Knowledge of the relationship between birch casebearer and white birch is important because it may lead to ways of lessening insect defoliation. This approach could involve managing a naturally occurring parameter. The knowledge gained from such a study could also enhance other herbivore-plant studies.

Coleophora serratella L. (Lepidoptera: Coleophoridae), the birch casebearer, is considered the most serious pest of white birch (Betula papyrifera Marsh.) in the Atlantic Provinces (Raske and Bryant, 1977b). Damage to the trees occurs when

larval birch casebearers destroy the newly emerging buds in early spring. Feeding of Instar III and IV larvae on the newly expanding leaves creates brown patches. This early season damage may cause twig, branch, or even tree mortality.

Birch wood has been used for railway ties, plywood, flooring, and furniture in the past. Today, the most extensive use of birch is for domestic fuelwood. However, in recent years there has been interest in Newfoundland birch because of increased world consumption and depletion of North American and European reserves. Birch plays a significant role in natural forest succession in Newfoundland. It regenerates readily, helps protect small softwoods from insects by acting as a buffering and filtering zone, and improves soil quality (van Nostrand, 1976). Birch is an early successional tree which grows rapidly. Fast growing trees help to prevent nutrients from leaching out of the soil by retaining them within their tissues. This serves to enrich the nutrient cycle for later successional, slower growing trees, such as softwood conifers which are of high value in Newfoundland's pulp and paper industry.

I.F: The Problem:

The white birch-birch casebearer system is ideal for studying damage-induced plant changes on a single herbivore within the same season because the most serious damage

inflicted on the tree is by Instar III and IV larvae, and is at a time of season when the spring buds are opening. My first hypothesis was that early season feeding damage in birch leaves by instar III and IV birch casebearer larvae will induce changes in the leaves that would negatively affect the late season Instar I and II larvae, as well as Instar III and IV in the following season.

The peculiar life history pattern of the birch casebearer is such that the faster growing Instar III and IV larvae consume the high nitrogen and moisture containing leaves early in the season, and the slower growing Instar I and II larvae feed on the late season, lower nitrogen and water containing leaves. My second hypothesis was to determine whether a relationship exists between the occurrence of the casebearer life history stages and changes in leaf water status, using water relations as an indication of physiological changes within the plant.

II. Materials and Methods

The hypothesis that early season damage induces changes in leaves which negatively affect late season larvae was tested by measuring nitrogen, phosphorus, leaf area, and duration of bud development and leaf senescence. These parameters were selected because they will indicate whether or not changes are occurring within the plant, and if they are damage induced. Effects of these changes on the birch casebearer population size were assessed through measurement of feeding damage, egg density, and population counts at various larval stages. Effects of plant changes on larval activity and size was measured by oviposition tests and headcapsule widths. Comparisons of these measurements were made among treatment groups which included control trees, artificially damaged trees, and two groups of insect damaged trees; light and severely defoliated trees.

The hypothesis that casebearer life history stages coincided with changes in leaf water status was tested by measuring fresh and dry leaf weights, fresh and dry specific weights, water content, and total water potential throughout the entire growing season. Developmental stages of both plant

and insect were then compared with changes in leaf water relations.

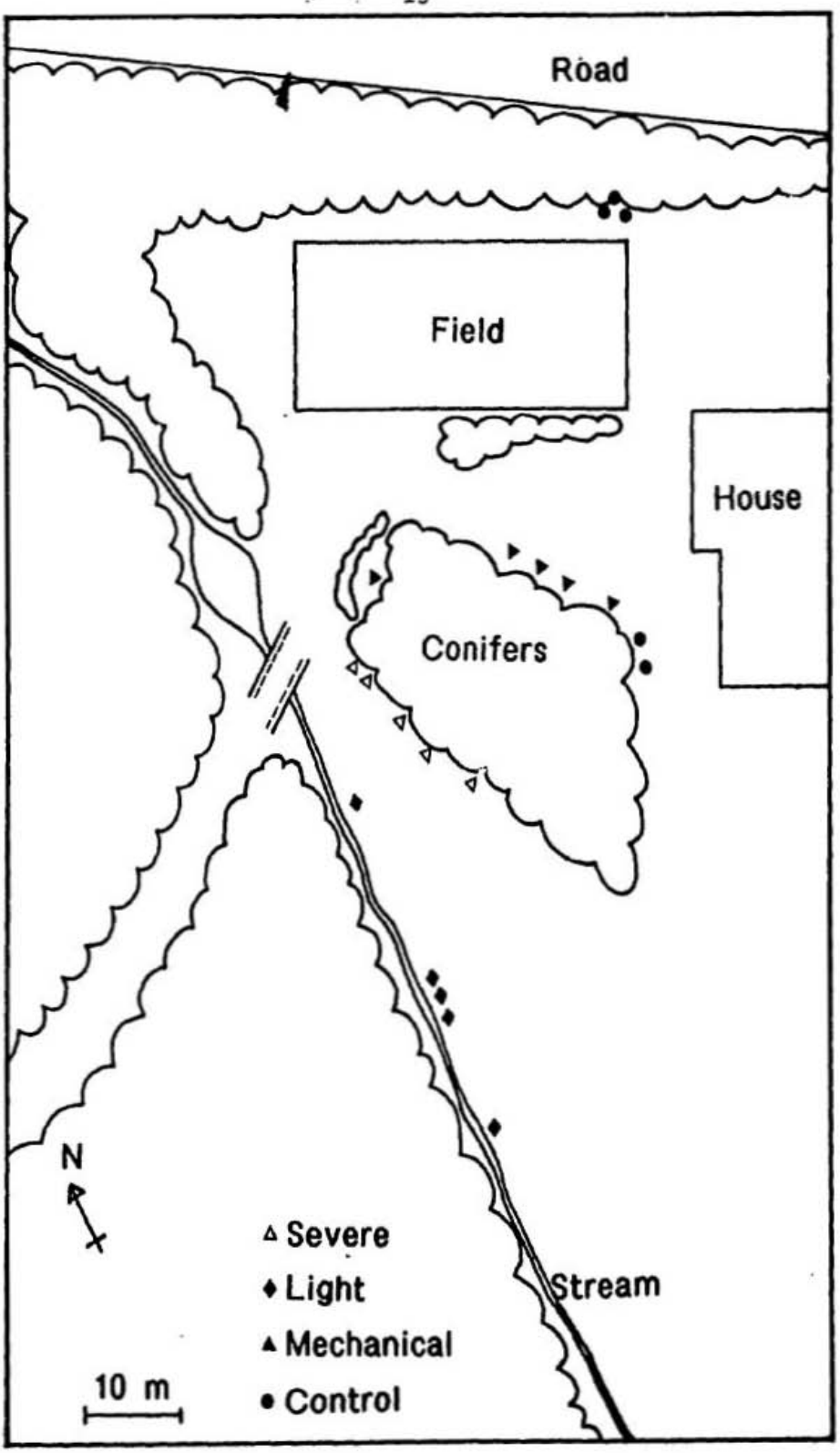
II.A: Study Design

Twenty white birch trees were located at the edge of a spruce-fir forest on Cochrane Pond Road, Goulds, Avalon Peninsula. Four groups of birch were selected, each consisting of five 1.5 to 3 meter high trees. For the most part the trees were positioned in groups along the forest edge (Figure 1). Lightly damaged trees were together at the edge of a stream slightly further away from the forest edge than the other groups. Three of the control trees were together on the opposite side of an open field, the other two were adjacent to mechanically damaged trees.

All trees initially contained approximately the same number of casebearers. Observation of trees from previous years indicated that low level infestation had occurred so manipulation of insect numbers was required. All manipulations occurred in the spring of the first growing season.

The degree of leaf damage on each tree was varied between groups. Control trees had no leaf damage. Insects were eliminated by applications of Malathion on June 4, 8, and 17, 1991. Malathion is not phytotoxic to white birch (Thomson, 1979-80). Mechanically damaged trees also were treated with

Figure 1: Map of study site showing position of trees.


Road
Field
House
Conifers
N
Severe
Light
Mechanical
Control
Stream
10 m

Malathion on the same dates but approximately 50% of the leaves were punctured three to four times with a 7.5 centimeter stainless steel nail approximately every two weeks for the entire summer. Five liters of Malathion in total (diluted at 20 mL / 3 L of water) was used on the ten trees on each of the three days. Lightly defoliated trees contained one to five casebearers per leaf, similar to initial conditions. The severely defoliated trees had their populations of casebearers augmented by tying twigs, containing approximately thirty overwintering casebearers per leaf, onto them on June 10, 1991. With the onset of warmer weather these casebearers moved to the newly opening buds. This created a large enough population of casebearers to severely damage the foliage. Group designation and type of treatment to which each was exposed, are summarized in Table 1.

Each tree in each group was divided into two layers, upper and lower halves of the crown, and into two aspects, north and south. Initially these quadrants were made to examine within tree variation on damage-induced changes.

Table 1: Type and amount of treatment applied to four treatment groups of five birch trees each in spring, 1991.

Group	Treatment
Control (C)	No artificial damage nor insects present - controlled by three applications of malathion.
Mechanically damaged (M)	Artificially damaged by puncturing 50% of leaves; No insects - controlled by three applications of malathion.
Lightly defoliated (L)	No changes made; natural low-level insect populations.
Severely defoliated (D)	Insects imported from Pasadena. Twigs with Instar II larvae were tied to study trees until diapause was over, and larvae crawled onto study trees.

II.B: Host Plant Development

II.B.i: Leaf Nutrients:

Leaf nitrogen and phosphorus levels were monitored for trees of each group in 1991 and 1992. Twenty leaves per tree (five from each quadrant) were sampled and analysed for nitrogen and phosphorus on 10 and 30 July, and 26 September, 1991
and 24 June, 1992. The first collection of each year was done at full leaf expansion to ensure consistency in the leaf developmental stage, as leaf age has been reported to affect nitrogen levels (Mattson, 1980). Leaves were sampled by cutting the base of the petiole with a razor blade. Leaves were collected into plastic bags, and later air dried in a lab for four days. The analysis of both nitrogen and phosphorus on pooled leaves per tree was done by the standard Kjeldahl method (Bradstreet, 1965) in Forestry Canada lab, St. John's, NF, Canada.

II.B.ii: Leaf Area:

Leaf area refers to the entire surface area of a birch leaf excluding the petiole. Total leaf area was measured in the first season to form base-line values for comparing subsequent changes in leaf area, and in the second season to examine possible plant compensation to herbivory. Feeding damage was measured concurrently with leaf area. Twenty leaves per tree,

five per quadrant, were selected and their surface areas determined. A transparent plastic grid, divided into square millimeters, was placed over each leaf and the number of square millimeter blocks that covered each of the leaves and parts of the leaf damaged by casebearer feeding were counted. In 1991 the leaves remained on the tree while areas were measured to prevent unnecessary damage which may affect the tree's response. In 1992, the leaves were removed since the study was coming to an end. Removal of the leaves also allowed leaf area to be determined easily and faster by a Mop 3 digital analyser. Outlines of leaves on paper were placed on glass covering a digitizing tablet. A mechanical cursor was then used to trace the outline of the leaf. Connections between cross hairs on the cursor and the digitizer below it determined the area traced and a digital read out was obtained.

II.B.iii: Bud Development and Leaf Senescence:

Observations of bud development and leaf senescence were made to compare the effects of differing levels of damage on leaf development. Bud development refers to the length of time it took for the buds to open from closed brown buds to fully expanded leaves in spring. Senescence refers to leaf die-back and abscission in the fall. The duration of senescence was measured as the time from which green leaves on

the tree began to change color until all leaves had fallen from the tree.

Length of the new terminal shoots was measured with a ruler (cm), and the number of buds per long shoot counted. Ten branches per tree from the center of the crown were measured. This was done in spring, 1992. Criteria for recognizing the categories of developing buds were (Senn et al, 1992):

1 = closed, brown buds,

2 = little green visible,

3 = expanding leaves, and

4 = expanded short-shoots.

Criteria used to measure rate of leaf senescence at the end of the season were:

1 = all leaves green,

2 = green leaves with minor changes to yellow/brown,

3 = equal numbers of green and yellow leaves,

4 = all leaves non-green, and

5 = a considerable number of leaves lost.

II.C: Water Relations

Comparisons were made between the occurrence of Instar I and II larval stages of casebearer and changes in leaf water relations. The time of day when leaves are at maximum water content and maximum water potential is usually pre-dawn (Kozlowski et al, 1991). A measure of leaf water relations

was required as they change with physiological activities within the plant, rather than with weather conditions, so pre-dawn was the optimal sampling time. This reduced variation in weights and water potential due to changes in weather conditions. Leaves were sampled at breast height and by age class to reduce variation because of location of the leaf on the tree. Young leaves were defined as the second leaf from the tip of long shoots. Medium-aged leaves were mature leaves, which occurred at the base of the long shoots; that is, those which were first to emerge on the long shoots in the spring. Old leaves were those which were first formed in the spring on the short shoots that were located near the base of the branch.

Three leaves from each age class, from each of six trees were collected into dry, plastic bags and kept on ice until transported to a lab where they were weighed by a Precision mechanical Mettler Balance. Leaves were then dried in a 50° C oven for 72 hours, and weighed for dry weights. Water content of a leaf was determined by subtracting its dry weight from its fresh weight. Water content, as a percentage of fresh weight, was obtained by subtracting dry weight from fresh weight, and dividing by fresh weight.

To provide a standard weight per millimeter, fresh weight of a leaf in milligrams was divided by the leaf surface area measured in square millimeters. Similarly, dry specific

weight of a leaf is the dry weight per square millimeter. This reduced the variation in weights caused by variation in leaf size.

Leaf total water potentials were obtained using a pressure bomb and compressed air tank (Noggle and Fritz, 1983). All measurements were made before sunrise approximately three times every two weeks. A pressure bomb is a stainless steel chamber capable of withstanding high pressures as air is slowly leaked into it from a compressed air diving tank. Leaves were placed such that the blade was inside the chamber, and the petiole protruding through the cover of the chamber. Sealant around the petiole at the cover entrance prevented air from leaking out. As the petiole of the leaf is cut from the tree, water in the xylem snaps back into the petiole to a distance which depends on the cohesive pressure exerted on the water within that leaf. Water in the petiole is forced back through the petiole until it reaches the cut surface by applying external pressure to the leaf blade. When water beads are visible on the cut petiole, the pressure required is recorded from the tank gauge.

Total water potential of medium aged leaves only were taken from June 22, full leaf expansion, until July 31. Younger leaves on the long shoots were not large enough to sample until the end of July. At this time water potentials of young, medium and old leaves were measured until senescence.

II.D: Population Estimates

Comparative indices of population sizes at various stages of the birch casebearer life cycle were made from all trees at various times over the two years. An indication of how populations change in relation to various changing host parameters was obtained by comparing indices among treatment groups.

II.D.i: Feeding Damage:

Percent feeding damage of Instar III and IV larvae was determined by measuring the surface area of the feeding blotch (mm^2), dividing by the total leaf surface area, and multiplying by 100. Leaves attached to the tree were assessed by placing a transparent squared millimeter grid over each leaf and counting the square millimeters covering each area measured. Five leaves per quadrant were chosen randomly. The number of leaves fed upon in each quadrant were counted, as well as the total number of leaves within the quadrant. This provided a measure of insect damage on each tree, as well as an index of the insect population size.

II.D.ii: Egg Density:

Egg density in the trees of each treatment group was determined to see if the various treatments and leaf characteristics had an effect on where female moths laid their

eggs.

Egg density was measured in July, 1991, by removing five leaves from each quadrant of each tree. Leaves were placed in plastic bags and returned to the lab. Number of eggs per leaf were counted under 10X magnification using a Wild Stereomicroscope.

II.D.iii: Overwintering Larvae:

Overwintering Instar II larvae were counted twice during winter 1991/92 to obtain estimates of early winter and late winter larval populations in each treatment group. The two counts were used to obtain an estimate of winter mortality. The first count was done on December 9, 1991, after the birch leaves had fallen, and the larvae had migrated to the twig axils for overwintering. The second count was done on April 20, 1992. Five branches per tree were chosen, each attached to the main trunk. The basal diameter of the branch was measured using Vernier Callipers. Larvae on each branch were counted and segregated into classes based on their position on the branch, namely: main axil; fork; and spur/bud. The main axil is the axil formed by the trunk and branch. A fork is the axil formed between any two twigs, or branch and twig. Spurs and buds were placed in the same category, and included all short-shoot spurs and bud axils.

II.D.iv: Pupal Estimates:

Number of pupae were counted in July, 1992, as an indication of population sizes for each treatment group. One branch per tree with approximately the same basal diameter and an equal number of smaller twigs was selected, and the number of pupae per entire branch was counted.

II.D.v: Instar I and II:

Instar I mines and Instar II larvae per branch were counted on twenty branches in September, 1992 to provide an estimate of population size only. The mines were located on the same leaves onto which the eggs were laid (Cochran, 1970). This provided an indication of the leaf age class onto which the female moth laid her eggs. Instar II larvae found on the same branches as the mines, were also counted to provide a measure of the survival of the larvae.

II.E: Effects of Plant Changes on Insect

II.E.i: Oviposition tests:

Choice tests were carried out with female moths in 1992. Each of three one meter by one meter fine mesh cages contained three plastic containers filled with clay. A birch or alder twig with ten to fifteen leaves was placed in each of two containers. The third container was saturated with water to

increase humidity in the cages. Twenty to thirty pupae were placed in each cage. Twigs were replaced approximately every three days to maintain freshness. Choices in one cage included one container with a birch twig high in nitrogen, and another container with a birch twig low in nitrogen. Similarly, another cage contained alder and birch twigs supplied to larvae that previously fed on alder, and another cage with alder and birch leaves supplied to larvae that previously fed on birch. Six trials (two of each choice) were done in a 15° C growth chamber with 18:6 hour daylight regime, and six trials (two of each choice) were later tested in a 14:10 hour regime. Three other trials were tested in the field adjacent to birch trees.

II.E.ii: Headcapsule Widths:

Headcapsule widths of Instar II larvae were measured in July, 1992, to determine if the treatments had an effect on larval size. Ten larvae per tree were removed from mid canopy level, placed in a vial, and returned to the lab. The headcapsule was removed from the larva and placed ventral side down. Distance between the two widest points on the headcapsule was recorded as the width. An eyepiece micrometer on a Wild Stereomicroscope was used to measure the widths.

II.F: Statistics:

Statistical analysis of the results was done on Minitab, version 7.2. Graphs were created using SigmaPlot, version 4.10. All data were screened for normality of distribution. Transformations were performed on egg density and percent feeding data. Egg density was transformed by square root, and percent feeding was subjected to arc sine (square root) transformation. Both were then subjected to two-way analysis of variance between treatment and canopy level for egg density, and between treatment and quadrant for feeding. Two-way analysis of variance was also used for leaf nitrogen and phosphorus levels to compare treatment and time of season. Two-way analysis of variance was also used for leaf area to compare treatment and quadrant.

One-way analysis of variance was used to compare treatments for long-shoot length and number of buds, overwintering Instar II larval estimates, and headcapsule widths of Instar III larvae. All analysis of variance testing used a maximum probability value of 0.05, and comparisons among treatments were made using confidence limits. All correlation analyses used Pearson's Correlation Coefficient Analysis.

III. Results

III.A: Host Plant Development

III.A.i: Nitrogen:

Levels of leaf nitrogen were highest in the spring (July 10), dropped sharply to mid summer (July 30), then remained constant or were slightly lower in September, 1991 (Table 2, Figure 2). Early season nitrogen levels for all treatment groups were significantly higher in 1992 than in 1991 ($P<0.05$) (Table 3). Early season 1992 nitrogen levels of control trees were significantly higher than lightly and severely damaged trees. Nitrogen in mechanically damaged trees was significantly higher than lightly damaged trees (Table 2).

On July 10, 1991, nitrogen levels in leaves of severely damaged and control groups were significantly higher than those in lightly damaged and mechanically damaged groups (Table 2, Figure 2). On July 30 nitrogen levels in severely and lightly damaged trees were significantly higher than those of mechanically damaged and control trees. Nitrogen levels in late season (September 26) did not differ significantly among

Table 2: Nitrogen levels (ppm) of birch leaves for 1991 and 1992 showing mean and standard deviation. [Means of each sampling time with same superscripts do not differ significantly, (P=0.05, ANOVA). Comparisons correspond to treatments at each time interval only].

Year	Time of Season	Treatment	Mean (ppm)	St. Dev.
1991	Early (July 10)	Severe	32079 [a]	6215
		Light	26952 [b]	3646
		Mechan.	27668 [b]	2173
		Control	32624 [a]	3664
	Mid (July 30)	Severe	23331 [a]	4483
		Light	23876 [a]	2664
		Mechan.	16979 [b]	3906
		Control	17267 [b]	5061
	Late (Sept.26)	Severe	19251 [a]	3011
		Light	19652 [a]	1754
		Mechan.	19876 [a]	2341
		Control	20747 [a]	3811
1992	Early (June 24)	Severe	39931 [a]	7309
		Light	39580 [a]	2590
		Mechan.	41686 [ab]	3572
		Control	48274 [cb]	2260

Figure 2: Leaf nutrients of white birch in 1991 for severely damaged (solid), lightly damaged (clear), mechanically damaged (lines rising to left), and control trees (hatched lines). A; leaf nitrogen levels (ppm), B; leaf phosphorus levels (ppm).

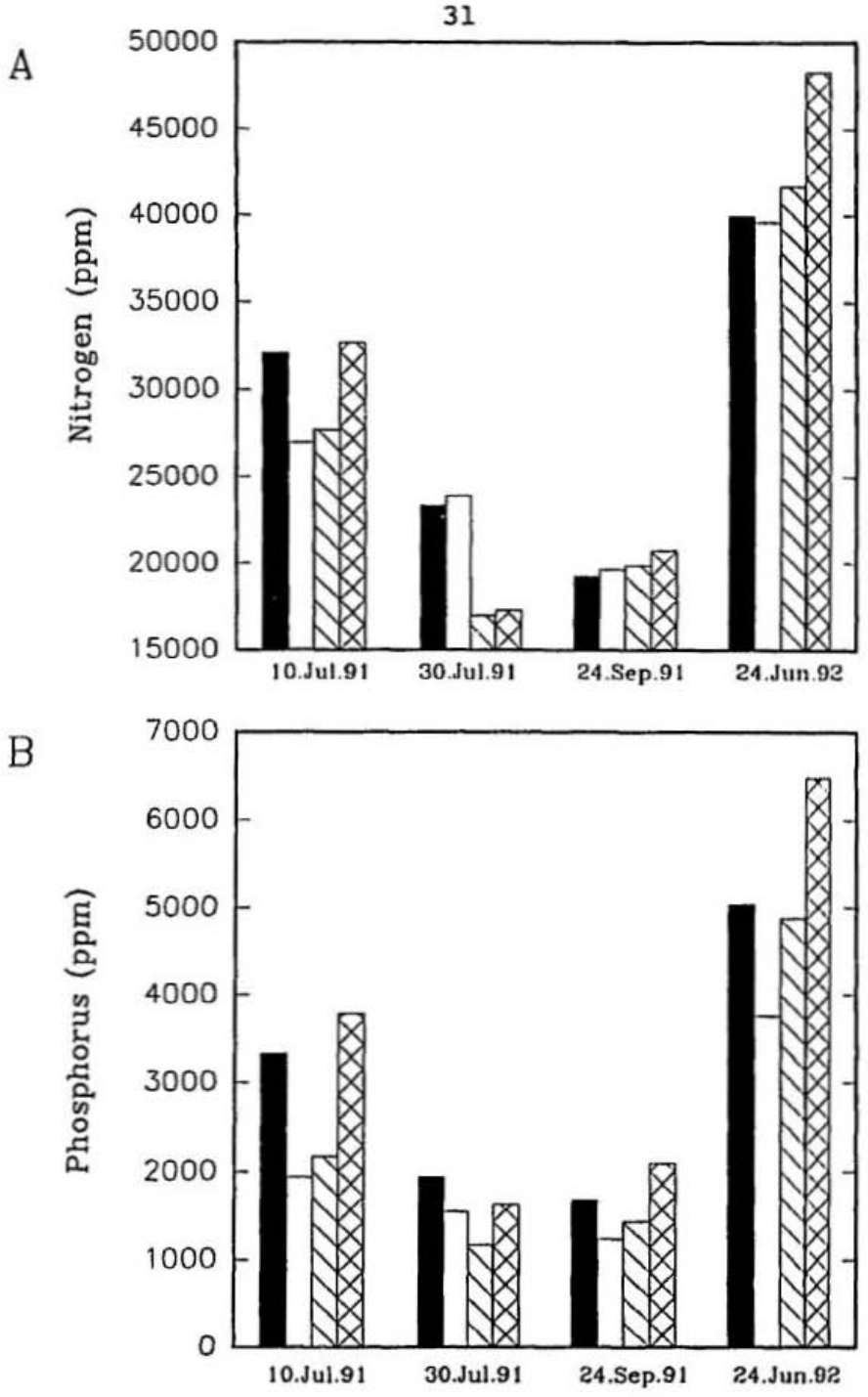

A
Nitrogen (ppm)
50000
45000
40000
35000
30000
25000
20000
15000
10.Jul.91
30.Jul.91
24.Sep.91
24.Jun.92
B
Phosphorus (ppm)
7000
6000
5000
4000
3000
2000
1000
0
10.Jul.91
30.Jul.91
24.Sep.91
24.Jun.92

Table 3: Nitrogen and phosphorus levels (ppm) for early season 1991 and 1992. [Mean nitrogen and phosphorus levels differed significantly between years (P=0.05, ANOVA).]

Year	Nitrogen		Phosphorus	
	Mean (ppm)	St. Dev.	Mean (ppm)	St. Dev.
1991	30673	5494	2831	928
1992	41918	5187	5033	1100

treatment groups. Nitrogen levels in mechanically damaged and control trees were significantly higher in late season than in mid season ($F_{(1,78)}=13.61, P<0.05$).

A two-way analysis of variance was performed to test the effects of treatment and time of season on 1991 nitrogen levels. There was a significant interaction effect ($F_{(6,204)}=5.33, P<0.05$). Time of season had a significant effect on leaf nitrogen levels ($F_{(2,204)}=172.3, P<0.05$), though treatment had no effect ($F_{(3,204)}=2.503, P>0.05$).

III.A.ii: Phosphorus:

Levels of leaf phosphorus showed a 1991 seasonal pattern similar to that of nitrogen (Table 4, Figure 2). Levels of phosphorus were significantly higher in early season 1992 than in 1991 (Table 4). Levels of leaf phosphorus in 1992 were significantly higher in control trees than in severely, lightly or mechanically damaged trees, and they were significantly higher in severely and mechanically damaged trees than in lightly damaged trees (Table 4).

Levels of phosphorus differed significantly among some treatment groups at each sampling period of 1991 (Table 4), similar to that of nitrogen. Phosphorus levels on July 10 were significantly higher in severely damaged and control groups than in lightly and mechanically-damaged groups. Phosphorus levels on July 30 were significantly higher in

Table 4: Phosphorus levels (ppm) of birch leaves for 1991 and 1992 showing mean and standard deviation. [Means of each sampling time with same superscripts do not differ significantly (P=0.05, ANOVA). Comparisons correspond to treatments at each time interval only.]

Year	Time of Season	Treatment	Mean(ppm)	St. Dev.
1991	Early (July 10)	Severe	3291 ^{a}	812
		Light	1941 ^{b}	212
		Mechan.	2172 ^{b}	281
		Control	3616 ^{a}	657
	Mid (July 30)	Severe	1939 ^{a}	541
		Light	1546 ^{b}	291
		Mechan.	1119 ^{c}	334
		Control	1439 ^{bc}	514
	Late (Sept.26)	Severe	1638 ^{a}	452
		Light	1233 ^{b}	284
		Mechan.	1432 ^{ab}	209
		Control	2089 ^{c}	469
1992	Early (June 24)	Severe	5030 ^{a}	786
		Light	3754 ^{b}	339
		Mechan.	4877 ^{a}	400
		Control	6473 ^{c}	431

severely damaged than control, lightly or mechanically-damaged trees. Phosphorus levels on September 26 were significantly higher in control than severely and mechanically-damaged trees, and both severely and mechanically damaged trees were significantly higher than lightly damaged trees.

Two-way analysis of variance on phosphorus levels showed that there was a significant interaction between treatment and time of season in 1991 ($F_{(6,204)}=11.2, P<0.05$). Both time of season ($F_{(2,204)}=167.0, P<0.05$) and treatment ($F_{(3,204)}=5.9, P<0.05$) had significant effects on leaf phosphorus levels.

Nitrogen and phosphorus levels were significantly positively correlated with each other ($n=264, r=0.803$) (Figure 3).

III.A.iii: Leaf Area:

Mean leaf area was significantly larger in 1992 than 1991 ($F_{(1,618)}=17.63, P<0.05$). Leaf area of all treatment groups increased from 1991 to 1992 except for the mechanically damaged groups (Figure 4). Differences in leaf areas among treatment groups in 1992 were smaller than those in 1991 (Figure 4), but treatment had a significant effect on leaf area in 1992 ($F_{(3,196)}=19.73, P<0.05$). Leaves on severely damaged trees were smaller than leaves on trees of the other three treatment groups (Table 5).

Comparisons by two-way analysis of variance were made among

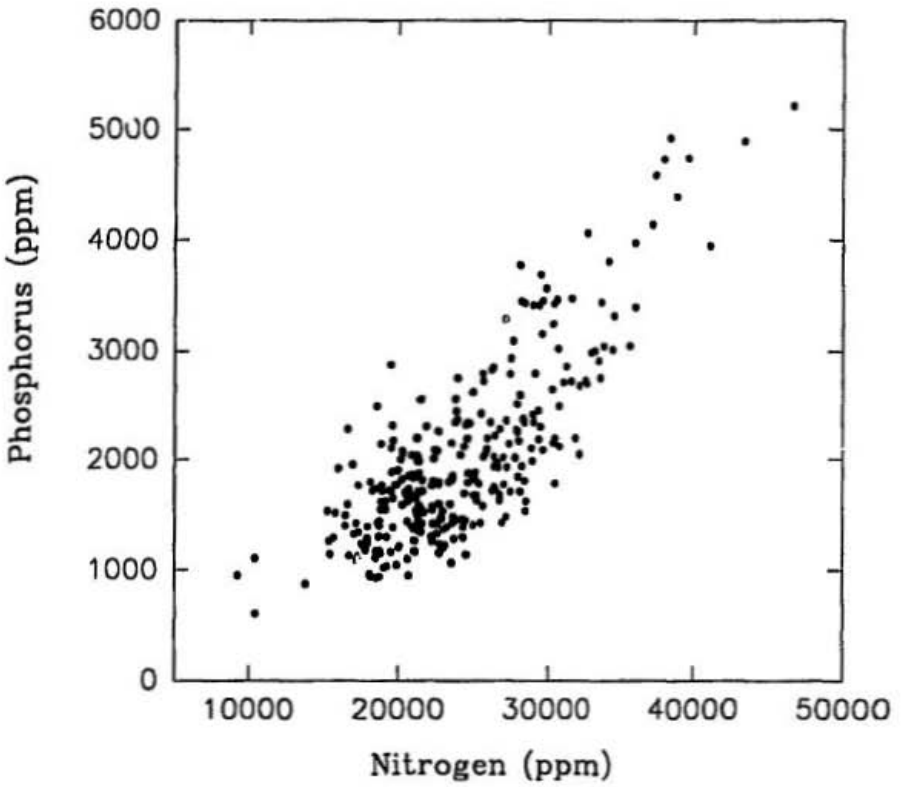


Figure 3: Relationship between nitrogen and phosphorus levels of white birch leaves (n=264, r=0.803).

Figure 4: Mean leaf area (mm^2) of four treatment groups in 1991 and 1992; severely damaged (solid), lightly damaged (clear), mechanically damaged (lines rising to left), and control trees (lines hatched).

Figure 5: Mean leaf area (mm^2) in 1991 of four quadrants comparing treatment groups; severely damaged (solid), lightly damaged (clear), mechanically damaged (lines rising to left), and control (lines hatched).

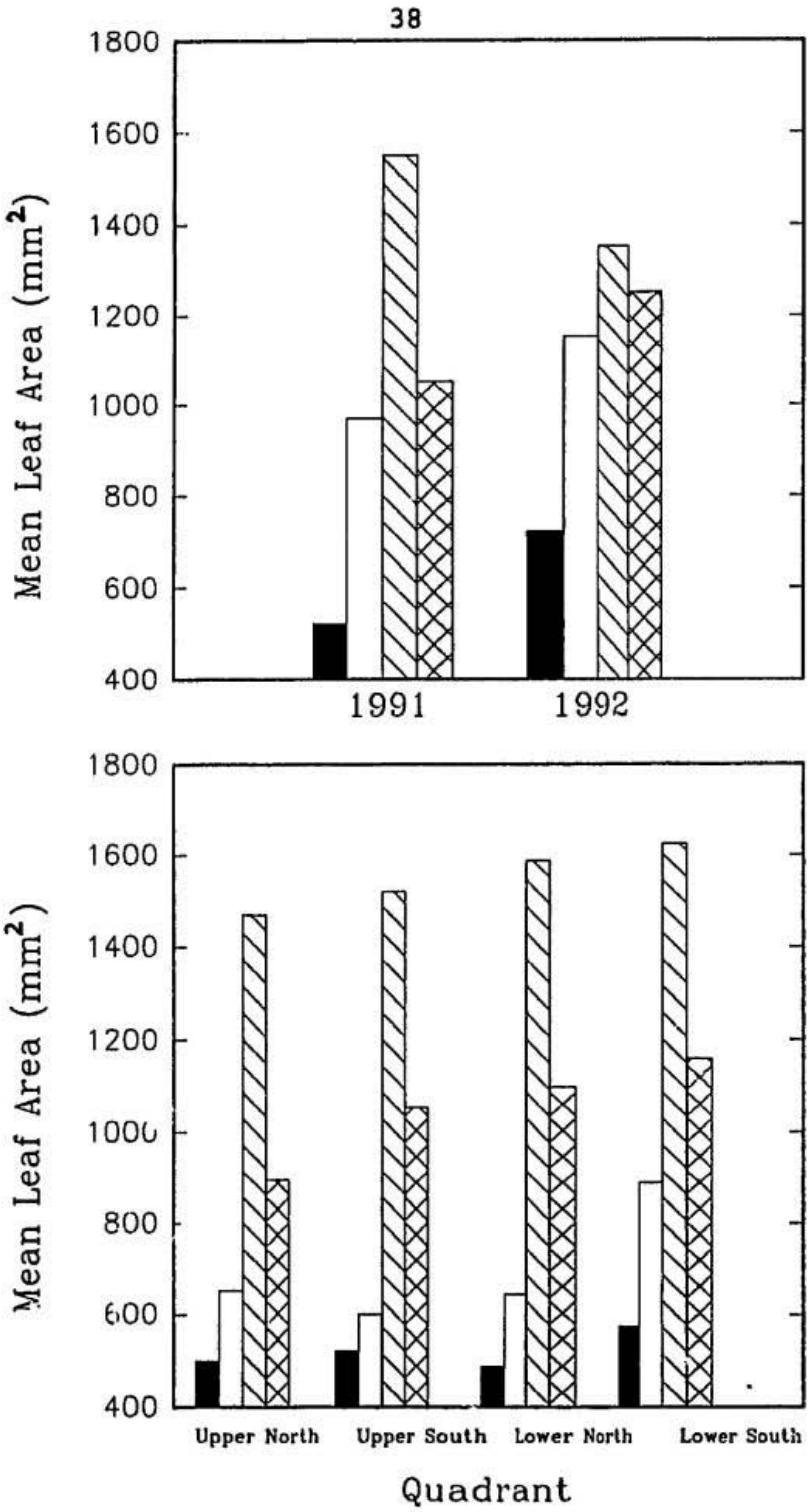

1800
1600
1400
1200
1000
800
600
400
Mean Leaf Area (mm²)
1991
1992
1800
1600
1400
1200
1000
800
600
400
Mean Leaf Area (mm²)
Upper North
Upper South
Lower North
Lower South
Quadrant

Table 5: Leaf areas (mm^2) for same quadrants between treatment groups for 1991 showing mean, standard deviation and analysis of variance. Quadrants are upper north (UN), upper south (US), lower north (LN), and lower south (LS).

Treatment	Mean (mm^2)	St. Dev.	ANOVA
Severe UN	499.6	313.8	NS
Light UN	651.0	413.0	
Severe US	521.7	363.2	NS
Light US	600.5	367.2	
Severe LN	487.5	249.2	P=0.025
Light LN	644.0	250.2	F=5.36
Severe LS	573.3	393.2	P=0.002
Light LS	890.0	325.8	F=10.31
Severe UN	499.6	313.8	P=0.000
Control UN	895.5	308.9	F=22.01
Severe US	521.7	363.2	P=0.000
Control US	1053.0	382.3	F=27.82
Severe LN	487.5	249.2	P=0.000
Control LN	1098.0	284.1	F=72.04
Severe LS	573.3	393.2	P=0.000
Control LS	1159.5	297.0	F=37.63
Severe UN	499.6	313.8	P=0.000
Mechanical UN	1469.0	498.0	F=77.11
Severe US	521.7	363.2	P=0.000
Mechanical US	1519.5	543.1	F=65.98
Severe LN	487.5	249.2	P=0.000
Mechanical LN	1587.0	619.6	F=79.31

Severe LS Mechanical	573.3	393.2	P=0.000
	1623.5	519.7	F=72.70
Light UN Control	651.0	413.0	P=0.022
	89[illegible].5	308.9	F=5.62
Light US Control	600.5	367.2	P=0.000
	1053.0	382.3	F=18.22
Light LN Control	644.0	250.2	P=0.000
	1098.0	284.1	F=35.94
Light LS Control	890.0	325.8	P=0.004
	1159.5	297.0	F=9.34
Light UN Mechanical	651.0	413.0	P=0.000
	1469.0	498.0	F=39.97
Light US Mechanical	600.5	367.2	P=0.000
	1519.5	543.1	F=49.13
Light LN Mechanical	644.0	250.2	P=0.000
	1587.0	619.6	F=49.78
Light LS Mechanical	890.0	325.8	P=0.000
	1623.5	519.7	F=35.76
Control UN Mechanical	895.5	308.9	P=0.000
	1469.0	498.0	F=23.94
Control US Mechanical	1053.0	382.3	P=0.001
	1519.5	543.1	F=12.33
Control LN Mechanical	1098.0	284.1	P=0.001
	1587.0	619.6	F=12.86
Control LS Mechanical	1159.5	297.0	P=0.000
	1623.5	519.7	F=15.02

leaf areas of quadrants across all treatment groups in 1991. There was no interaction between quadrant and treatment on leaf areas in 1991 ($F_{(9,384)}=0.65, P>0.05$). Both quadrant ($F_{(3,384)}=3.86, P<0.05$) and treatment ($F_{(3,384)}=147.31$) had significant effects on leaf area. Generally, leaves were largest in the lower south quadrant and smallest in the upper north quadrant (Figure 5). Leaf areas differed significantly only between upper north and lower south quadrants.

III.A.iv: Bud Development and Leaf Senescence:

Long-shoots were significantly shorter in severely damaged trees in 1992 than in the other treatment groups ($F_{(3,196)}=61.84, P<0.05$). Shoots were significantly shorter in control trees than in light and mechanically damaged trees, but there was no significant difference in shoot length between lightly and mechanically damaged trees (Table 6, Figure 6). Similarly, there were significantly fewer buds per long-shoot in severely damaged than in other treatment groups ($F_{(3,196)}=23.99, P<0.05$), and significantly fewer buds in lightly damaged than in control trees, but mechanically damaged and control treatment groups were not significantly different (Table 7). A significant positive correlation was found between shoot length and the number of buds on it (Figure 7) ($n=117$, $r=0.873$).

Buds developed later in severely damaged and control trees

Table 6: Long-shoot length (cm) of treatment trees in spring 1992 showing mean and standard deviation. [Means with same superscripts do not differ significantly (P=0.05, ANOVA).]

Treatment	Mean (cm)	St. Dev.
Severe	4.308 [a]	6.080
Light	18.166 [b]	8.104
Mechan.	18.714 [b]	5.583
Control	14.620 [c]	3.244

Table 7: Number of buds per long-shoot in spring 1992 showing mean and standard deviation. [Means with same superscripts do not differ significantly (P=0.05, ANOVA).]

Treatment	Mean (# buds)	St. Dev.
Severe	3.220 [a]	1.375
Light	5.780 [b]	1.250
Mechan.	5.240 [bc]	1.965
Control	4.800 [c]	1.678

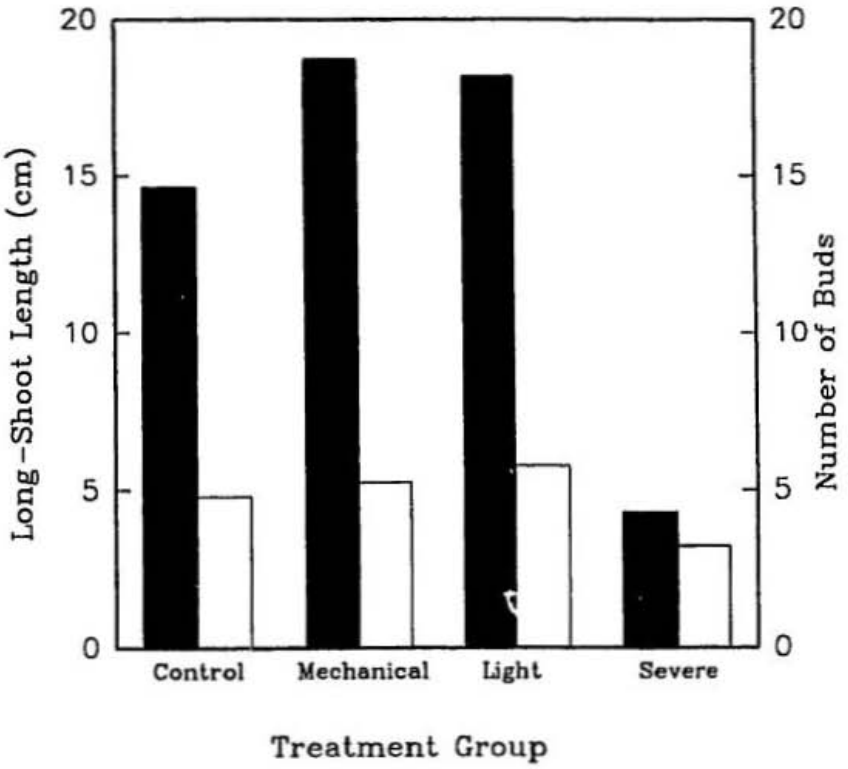


Figure 6: Growth of white birch trees of the four treatment groups in autumn, 1991. Measure of growth on y axis represents centimeters for long-shoot length (solid), and number of buds on each long-shoot (clear).

in spring 1992 relative to bud development of other treatment groups (Figure 8). Leaves of control trees senesced earlier than those of other treatment groups, and leaves of severely damaged trees senesced later than those of other treatment groups (Figure 9).

III.B.i: Water Relations

III.B.i: Medium Aged Leaves:

Although there was much variation in pre-dawn weights among samples, mean fresh and dry leaf weights on average increased throughout the growing season (Figure 10). Specific fresh and dry weights also increased throughout the growing season (Figure 11). Fresh specific weights increased until mid season, then levelled off, and dropped at the end of the season as leaves began to senesce. The dry specific weights showed a similar trend.

Water content of leaves decreased to mid season, then increased slightly before decreasing at the end of the season (Figure 12). Total water potential increased at the beginning of the season, remained fairly consistent until about mid to late season, and then began to oscillate until a final drop at the onset of leaf senescence (Figure 13).

III.B.ii: Young and Old Leaves:

Fresh and dry weights of young and old leaves showed

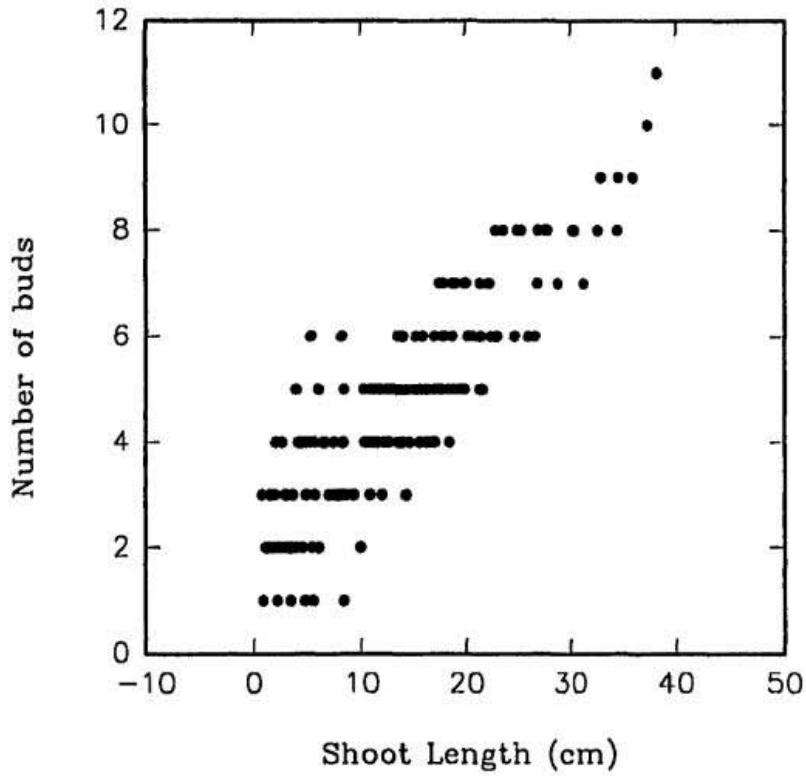


Figure 7: Relationship between number of buds and long-shoot length (n=117, r=0.873).

Figure 8: Development of spring buds in 1992 for four treatment groups; severely damaged (open squares), lightly damaged (filled triangles), mechanically damaged (open triangles), and control (filled circles). Bud development scale represents the following: 1=closed, brown buds, 2=little green visible, 3=expanding leaves, 4=expanded short-shoots.

Figure 9: Senescence of white birch leaves in Fall 1992 for four treatment groups; severely damaged (open squares), lightly damaged (filled triangles), mechanically damaged (open triangles), and control (filled circles). Leaf senescence scale represents the following: 1=all leaves green, 2=green leaves with minor changes to yellow/brown, 3=equal numbers of green and yellow leaves, 4=all leaves non-green, 5=a considerable number of leaves lost.

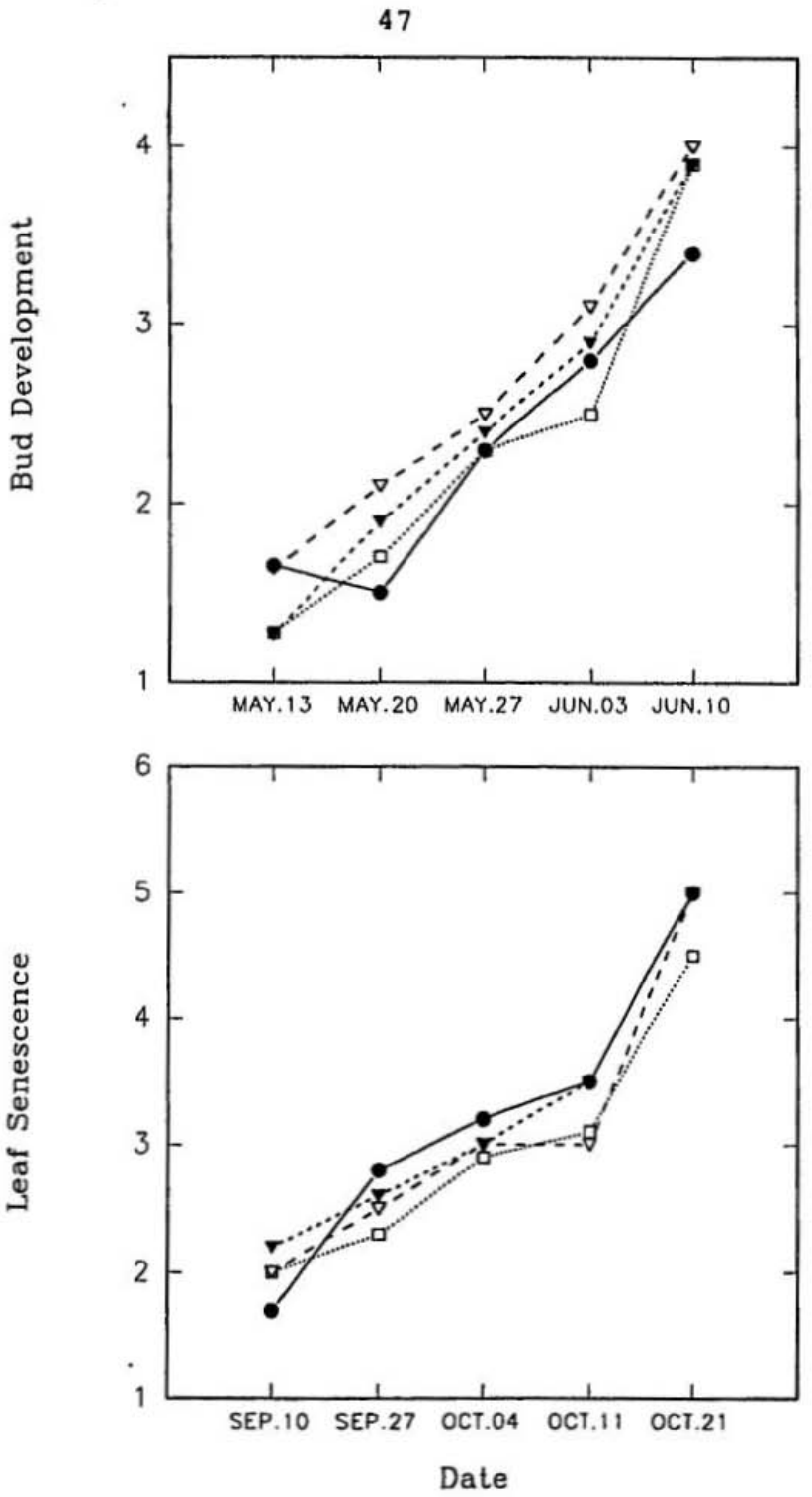

Bud Development
4
3
2
1
MAY.13
MAY.20
MAY.27
JUN.03
JUN.10
Leaf Senescence
6
5
4
3
2
1
SEP.10
SEP.27
OCT.04
OCT.11
OCT.21
Date

Figure 10: Weight of medium aged (filled circles, solid line), young (open triangles, dashed line) and old (closed triangles, dashed line) white birch leaves in 1992. A; leaf fresh weight (mg), B; leaf dry weight (mg).

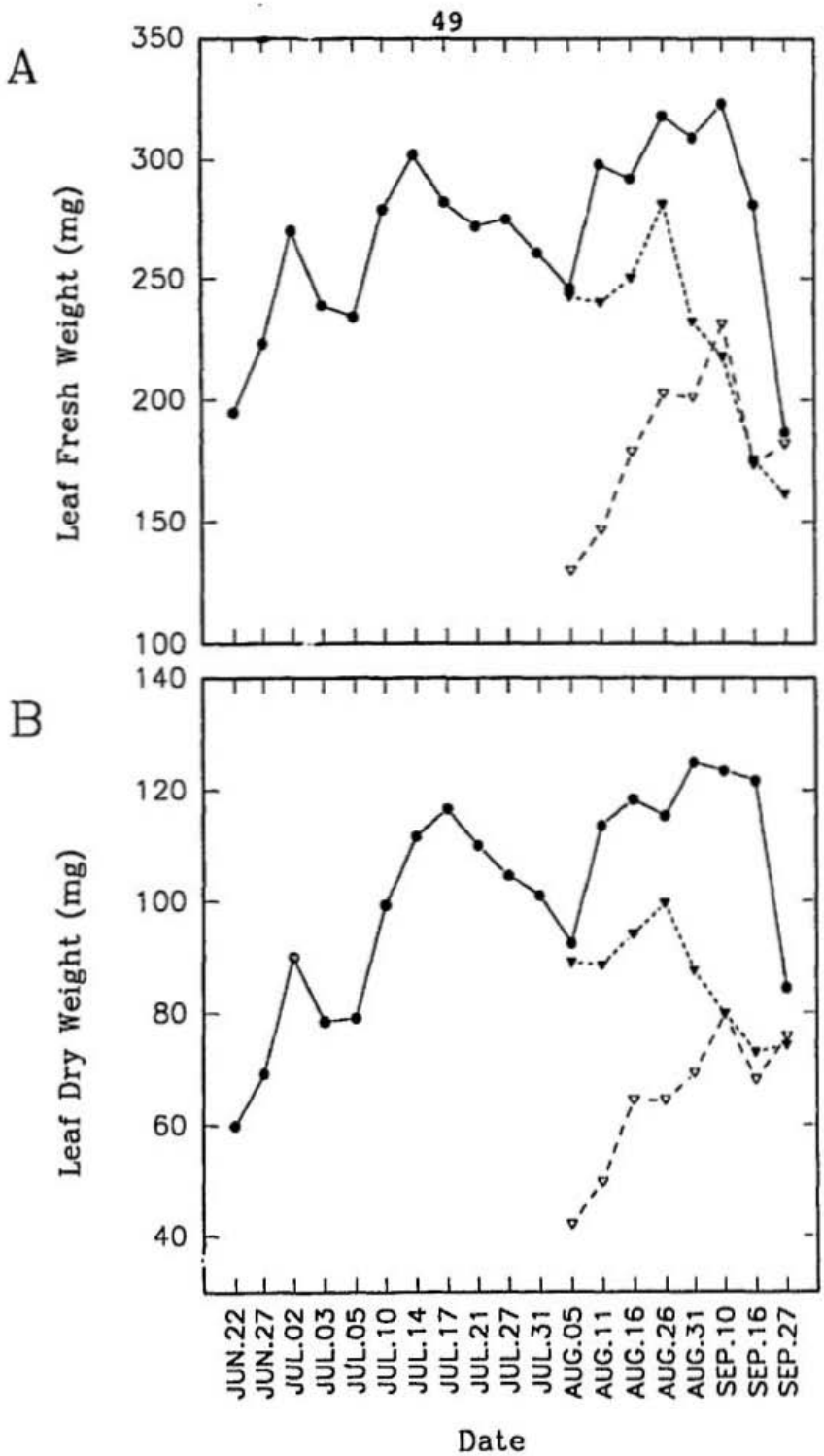
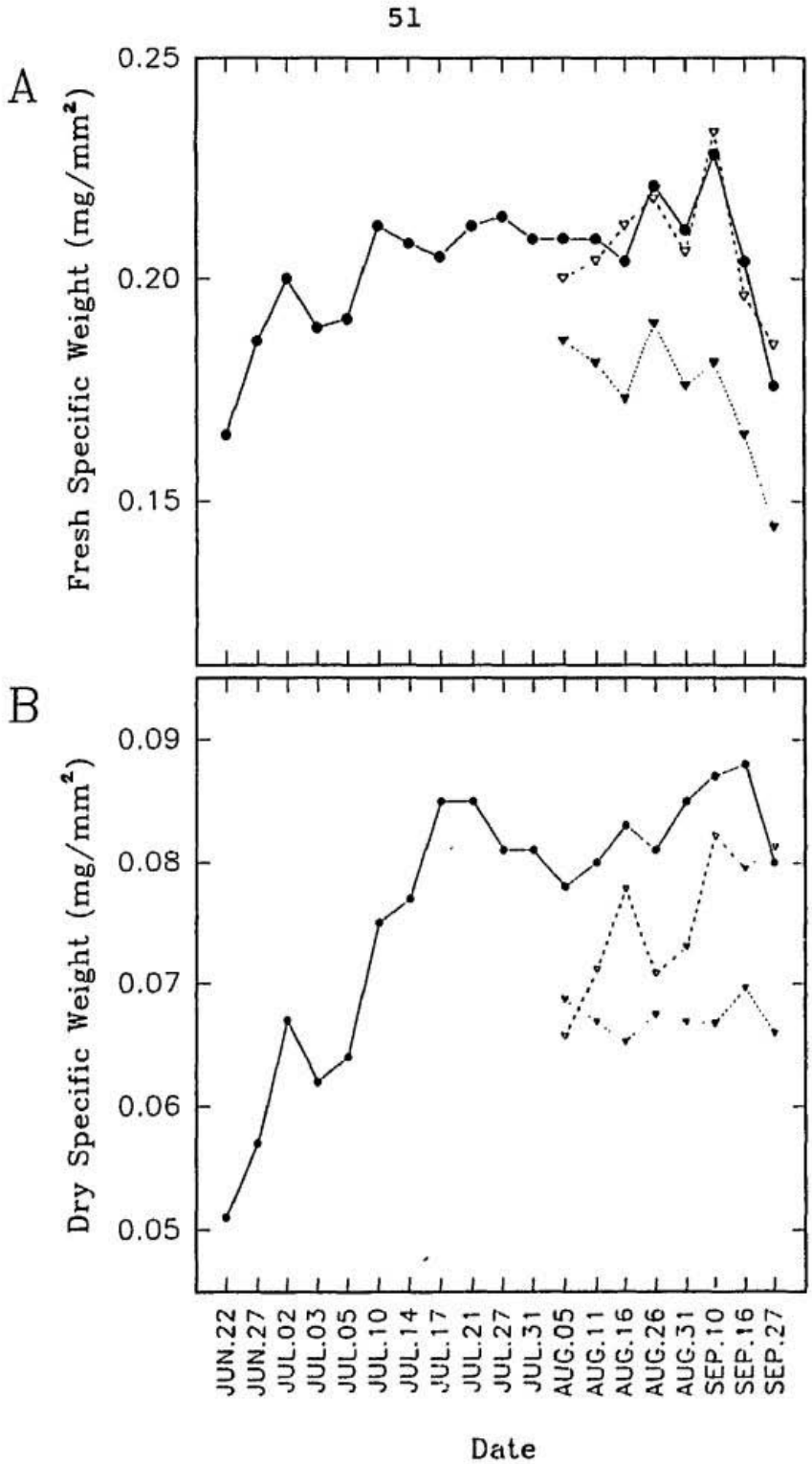

A
B
Leaf Fresh Weight (mg)
Leaf Dry Weight (mg)
350
300
250
200
150
100
140
120
100
80
60
40
JUN.22
JUN.27
JUL.02
JUL.03
JUL.05
JUL.10
JUL.14
JUL.17
JUL.21
JUL.27
JUL.31
AUG.05
AUG.11
AUG.16
AUG.26
AUG.31
SEP.10
SEP.16
SEP.27
Date

Figure 11: Specific weight (mg/mm^2) of medium aged (closed circles, solid line), young (open triangles, dashed line), and old (closed triangles, dashed line) white birch leaves in 1992. A; fresh specific weight, B; dry specific weight.


A
Fresh Specific Weight (mg/mm²)
0.25
0.20
0.15
B
Dry Specific Weight (mg/mm²)
0.09
0.08
0.07
0.06
0.05
JUN.22
JUN.27
JUL.02
JUL.03
JUL.05
JUL.10
JUL.14
JUL.17
JUL.21
JUL.27
JUL.31
AUG.05
AUG.11
AUG.16
AUG.26
AUG.31
SEP.10
SEP.16
SEP.27
Date

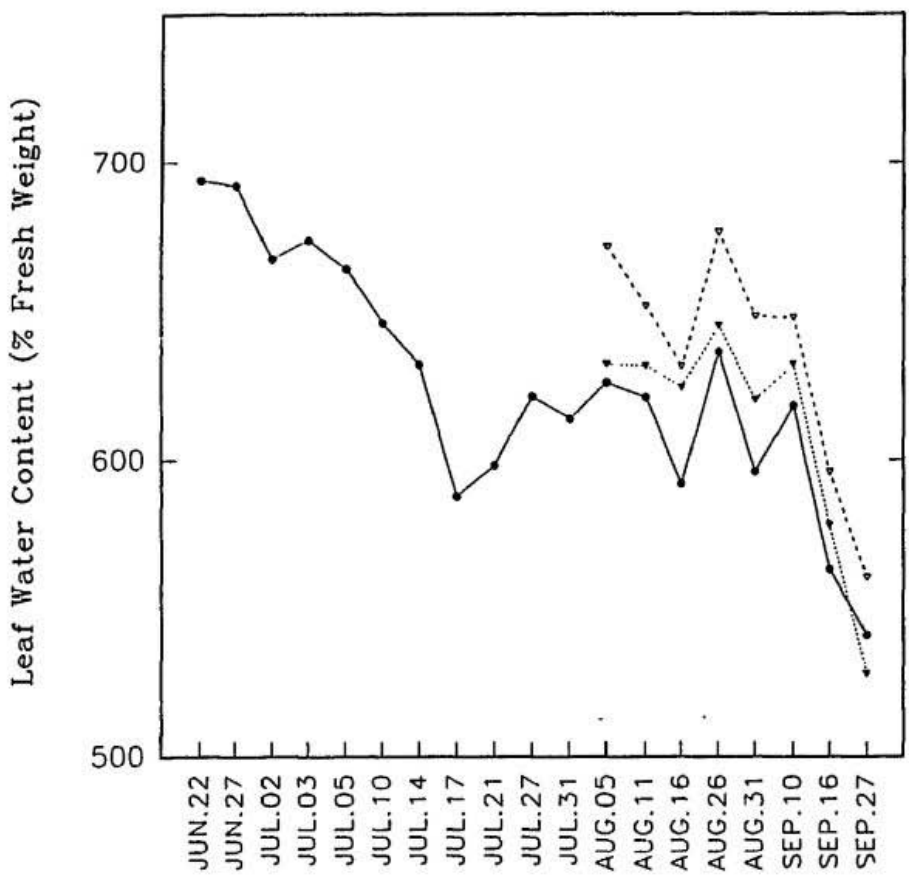


Figure 12: Water content (% fresh weight) of medium aged (solid circles, solid line), young (open triangles, dashed line), and old (closed triangles, dashed line) white birch leaves in 1992.

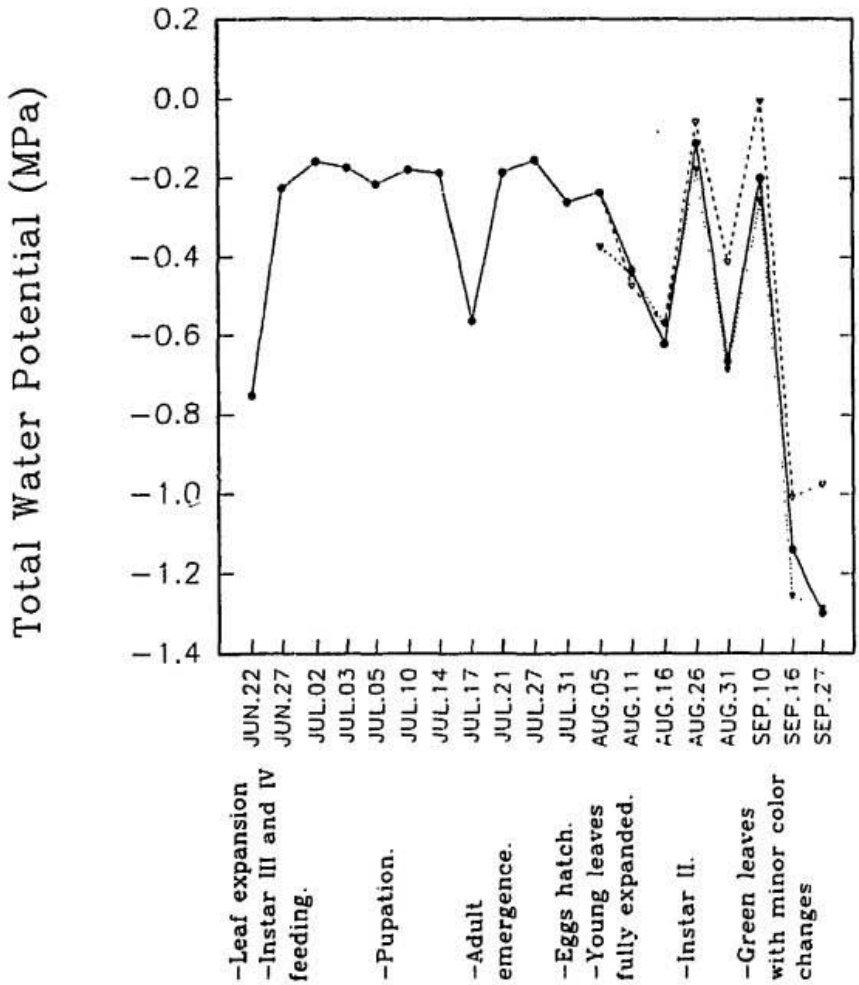


Figure 13: Total water potential (MPa) of medium aged (solid circles, solid line), young (open triangles, dashed line), and old white birch leaves (solid triangles, dashed line) in 1992, showing relationship with occurrence of leaf developmental stages and casebearer life history stages.

different late seasonal trends (Figure 10). Weights of young leaves increased until September 10, the approximate date at which senescence of medium-aged leaves occurred, and then they declined. Weights of the old leaves increased only slightly until August 26, before dropping sharply. The decrease in old leaf weights occurred about two weeks before those of the young leaves, and about one to two weeks before those of medium-aged leaves.

Specific fresh weights of both young and old leaves began to drop on September 10 (Figure 11). Specific dry weights of young leaves increased to about September 10, whereas those of the old leaves remained fairly constant to September 10.

Water content of both young and old leaves dropped sharply from September 10 to 27 (Figure 12). Total water potential was slightly higher in the older leaves than in the younger leaves near the end of the season, although the difference was not significant (Figure 13).

III.C: Population Estimates

III.C.i: Feeding Damage by Instar III and IV Larvae:

Percent feeding damage on leaves of severely and lightly damaged trees was significantly lower in 1992 than 1991 ($F_{(1,318)}=82.61, P<0.05$), and was higher in mechanically damaged and control trees (Figure 14). Percent feeding in 1991 was

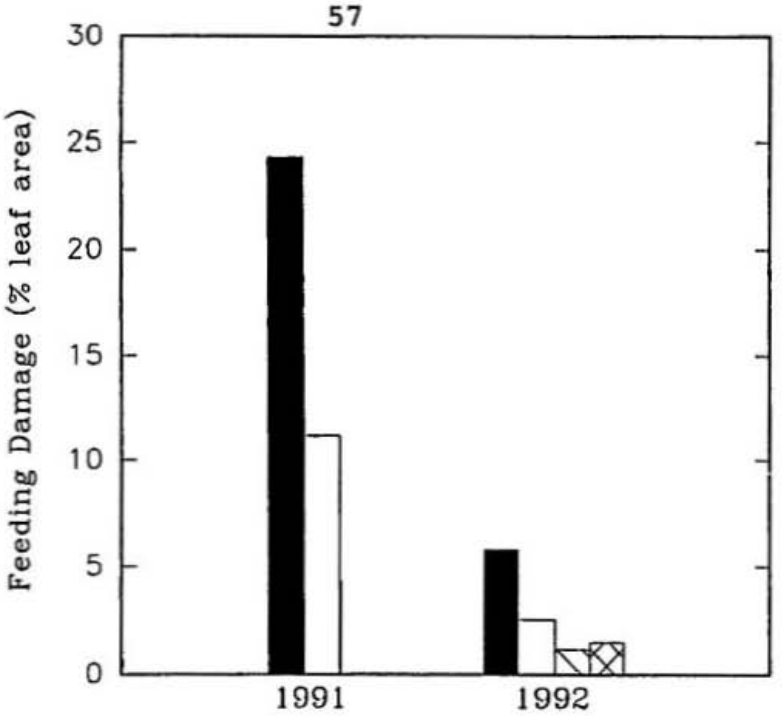
significantly lower in lightly damaged than severely damaged trees ($F_{(1,218)}=28.49, P<0.05$). Percent feeding damage in severely damaged trees remained significantly higher than that in lightly damaged trees in 1992 ($F_{(1,218)}=28.49, P<0.05$) (Table 8).

Percent feeding damage in spring of 1992 differed significantly between severe and all other treatments, and between light and mechanically damaged trees, but not between light and control, or mechanical and control trees (Table 8).

Percent feeding damage in 1991 was tested by two-way analysis of variance (after arc sine(square root) transformation of data) for effects of treatment and quadrant on feeding damage. There was no significant interaction effect but there was a significant effect of quadrant on feeding damage ($F_{(3,192)}=3.18, P<0.05$). Tree quadrant had no significant effect on feeding area of severely damaged trees ($F_{(3,116)}=0.93, P>0.05$) though it significantly affected feeding area of lightly damaged trees ($F_{(3,96)}=22.27, P<0.05$). Upper south quadrant was higher than other quadrants (Table 9). Treatment also affected feeding area significantly ($F_{(1,192)}=32.75, P<0.05$) (Table 10, Figure 15). Severely damaged treatment groups had larger feeding areas than lightly damaged groups (Figure 15).

Figure 14: Percent feeding damage (% leaf area) in 1991 and 1992 by Instar III and IV larvae comparing treatment groups; severely damaged (solid), lightly damaged (clear), mechanically damaged (lines rising to left), and control (lines hatched).

Figure 15: Percent feeding damage (% leaf area) in 1991 by Instar III and IV larvae, comparing the four quadrants in severely (solid) and lightly (open) damaged treatment groups.


Feeding Damage (% leaf area)
30
25
20
15
10
5
0
1991
1992

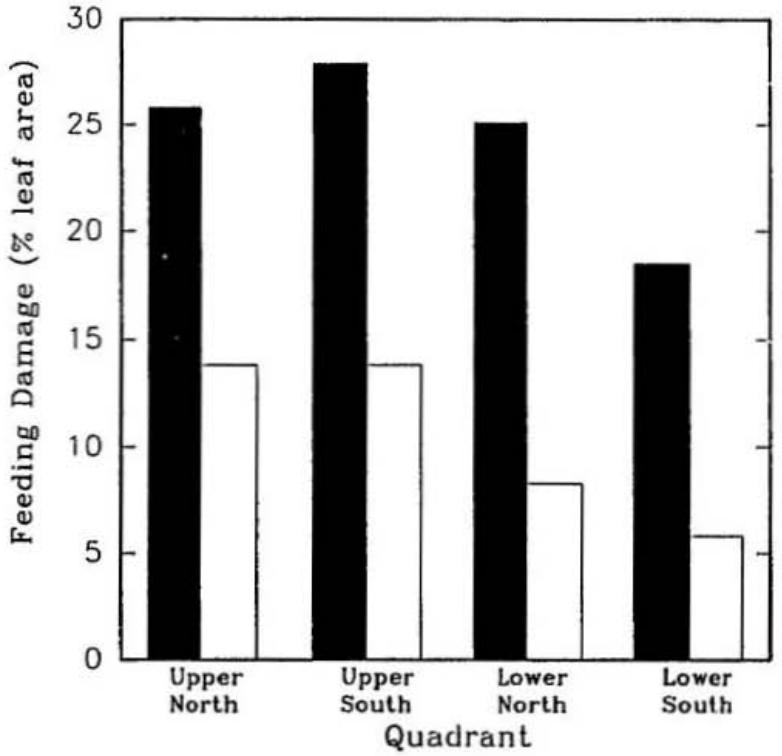

Feeding Damage (% leaf area)
30
25
20
15
10
5
0
Upper North
Upper South
Lower North
Lower South
Quadrant

Table 8: Percent feeding damage (arc sine$\sqrt{\%\ \text{feeding}}$) and total leaf area ($mm^2$) for 1991 and 1992 showing mean and standard deviation of all significantly different areas between treatment groups (P=0.05, ANOVA).

Treatment Groups	1991 Feeding Area (arc sin$\sqrt{\%fed}$)		1991 Total Leaf Area (mm^2)		1992 Feeding Area (arc sin$\sqrt{\%fed}$)		1992 Total Leaf Area (mm^2)	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Severe	48.2	28.6	520	332	19.4	15.6	730	466
Light	30.8	17.1	696	358	11.8	11.2	1159	347
Severe	-		521	332	19.4	15.6	730	466
Mechanical			1550	542	7.3	8.2	1364	420
Severe	-		521	332	19.4	15.6	730	466
Control			1052	330	7.7	9.8	1265	526
Light	-		696	358	11.8	11.2	1159	347
Mechanical			1550	542	7.3	8.2	1364	420
Light	-		696	358	NS		NS	
Control			1052	330				
Mechanical	-		1550	542	NS		NS	
Control			1052	330				

Table 9: Feeding damage (Arc sine $\sqrt{\%\ \text{leaf area}}$) for 1991 severely and lightly damaged treatment groups showing mean and standard deviation. Quadrants are upper north (UN), upper south (US), lower north (LN), and lower south (LS).

Treatment - Quadrant		Mean arc sine ($\sqrt{\%\text{leaf area}}$)	Standard Deviation
Severe	UN	49.47	29.64
Light	UN	33.64	22.66
Severe	US	52.77	36.20
Light	US	59.01	21.38
Severe	LN	49.75	24.34
Light	LN	27.28	11.33
Severe	LS	41.02	22.47
Light	LS	23.08	8.04

Table 10: Feeding damage (arc sine $\sqrt{\%\ \text{leaf area}}$) for 1991 severely and lightly damaged groups showing within tree (between quadrant) differences in mean and standard deviation.

Treatment - Quadrants		Mean (arc sin $\sqrt{\%\ \text{leaf area}}$)	Standard Deviation
Severe	UN	49.47	29.64
	US	52.77	36.20
Severe	LN	49.75	24.34
	LS	41.02	22.47
Severe	LN	49.75	24.34
	UN	49.47	29.64
Severe	LS	41.02	22.47
	US	52.77	36.20
Light	UN	33.64	22.66
	US	59.01	21.38
Light	LN	27.28	11.33
	LS	23.08	8.04
Light	LN	27.28	11.33
	UN	33.64	22.66
Light	US	59.01	21.38
	LS	23.08	8.04

III.C.ii: Egg Density:

A two-way analysis of variance to test for effects of treatment and canopy level on egg density showed that there was no interaction ($F_{(3,56)}=0.40, P>0.05$) but both treatment ($F_{(3,56)}=13.69, P<0.05$) and canopy level ($F_{(1,56)}=24.07, P<0.05$) significantly affected egg density.

Mean egg density was lowest in control (x=0.820, SD=0.515), higher in severely damaged (x=1.008, SD=0.910), then mechanically damaged (x=1.215, SD=1.420), and highest in lightly damaged trees (x=3.150, SD=2.261) (Figure 16). Lightly damaged trees had more eggs per leaf than the others.

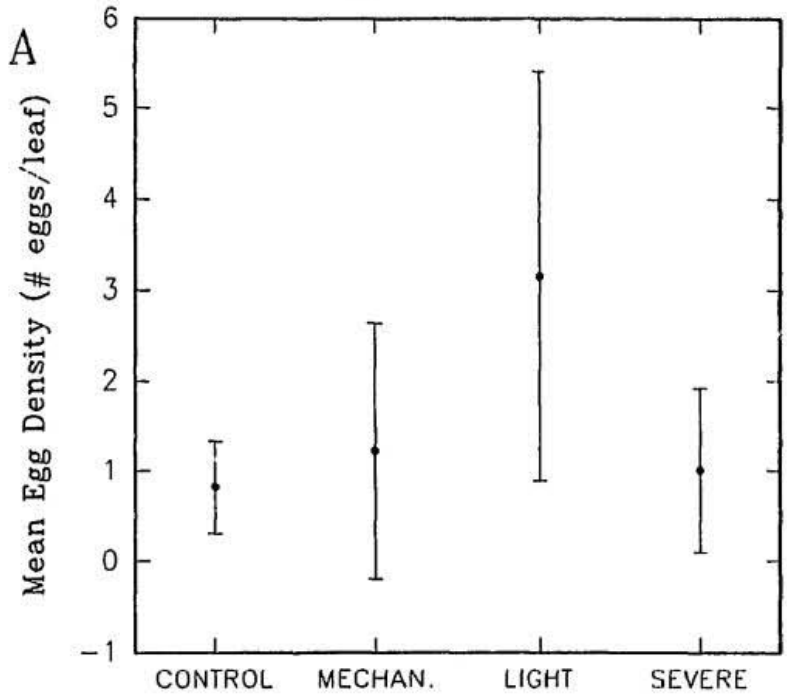
There were significantly more eggs per leaf in the upper crown than in the lower (P=0.000, F=15.11), (upper: x=2.176, SD=2.054) (lower: x=0.869, SD=0.729) (Figure 16). There was no significant difference in egg density between the north and south aspects of the trees.

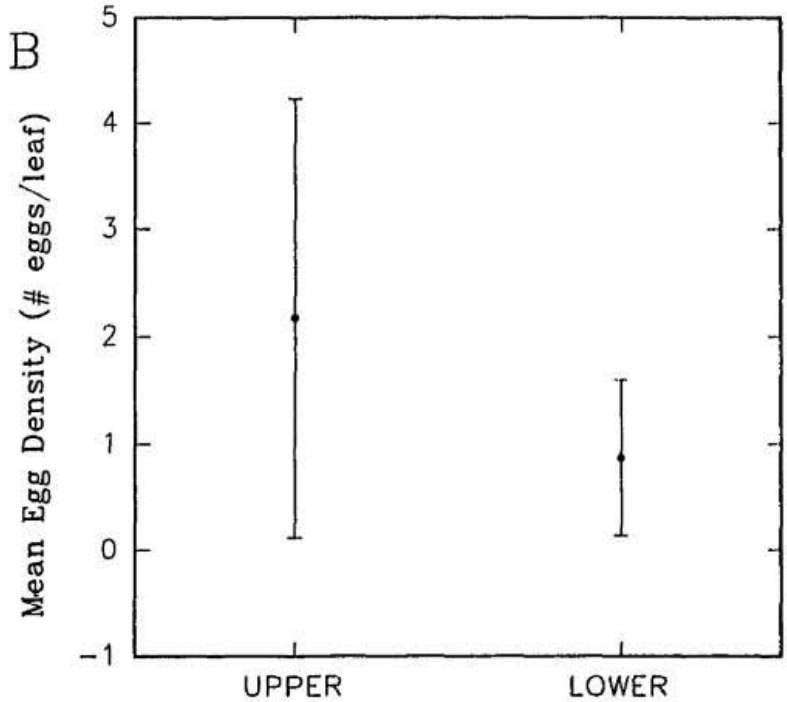
A significant positive correlation was obtained between the number of eggs per leaf and the 1991 mid-season nitrogen levels (Figure 17) (n=80, r=0.24).

III.C.iii: Overwintering Larvae:

The December estimate showed no significant difference ($F_{(3,59)}=2.40, P>0.05$) in overwintering larvae in total axils (spurs and forks) among treatment groups. The trend of the numbers of overwintering larvae was lowest in mechanically

Figure 16: Egg density of birch casebearer (mean # eggs/leaf) for 1991. Vertical bars represent standard deviations around the mean. A; differences between treatment groups. B; differences between upper and lower crown levels.


A
Mean Egg Density (# eggs/leaf)
6
5
4
3
2
1
0
−1
CONTROL
MECHAN.
LIGHT
SEVERE


B
Mean Egg Density (# eggs/leaf)
5
4
3
2
1
0
−1
UPPER
LOWER

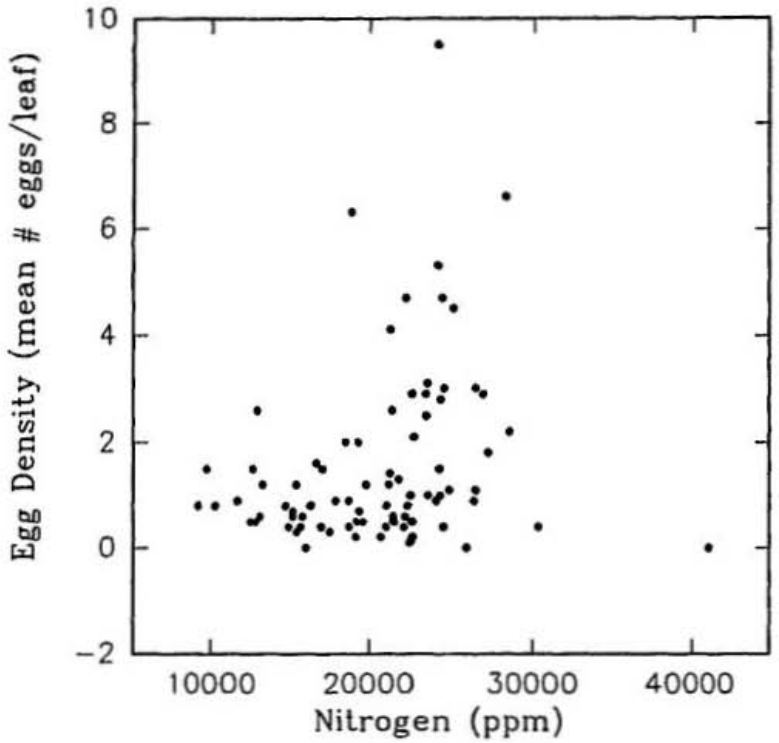


Figure 17: Egg density and mid-season leaf nitrogen levels in 1991 (n=80, r=0.24).

damaged, higher in control, even higher in severely damaged, and highest in lightly-damaged groups (Figure 18). There was a significant correlation between the number of overwintering larvae and the basal diameter of the branch (Figure 19) (n=61, r=0.36). Also, there were significantly more larvae in the spurs on severely and lightly damaged trees in December than on mechanically damaged and control trees ($F_{(3,59)}=7.23, P<0.05$).

There was no significant difference among treatments for the numbers of larvae overwintering in the forks ($F_{(3,59)}=0.5, P>0.05$).

The number of larvae in March overwintering in axils (spurs and forks) was significantly higher in the lightly damaged trees ($F_{(3,59)}=5.29, P<0.05$) than the other three groups (Figure 18).

The March counts showed significantly more larvae in lightly damaged treatment groups in both forks ($F_{(3,59)}=4.8, P<0.05$) and spurs ($F_{(3,59)}=4.52, P<0.05$). March larval counts were significantly lower than the December counts ($F_{(1,124)}=14.15, P<0.05$).

III.C.iv: Instar I and II Larvae:

Medium aged and older leaves contained a larger mean number of mines per leaf than the younger leaves at the end of the 1992 season, although there was no significant difference ($P>0.05$) (Table 11). The number of instar II larvae was

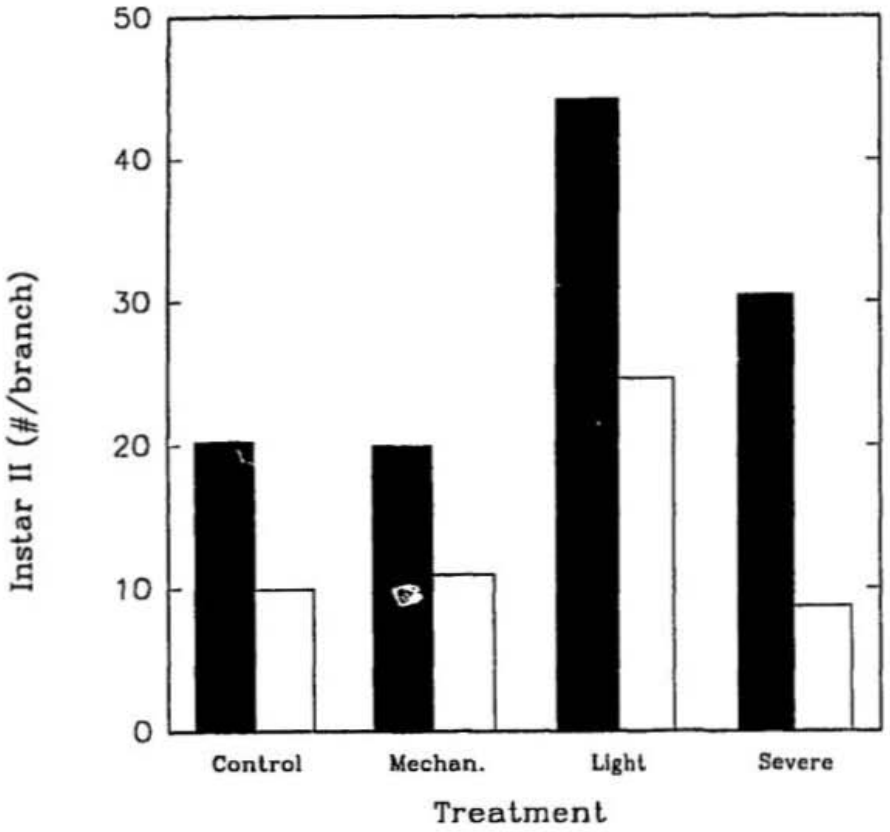


Figure 18: Birch casebearer overwintering Instar II larvae (mean # larvae/branch) in December, 1991 (solid bars) and March, 1992 (open bars), showing differences among treatment groups.

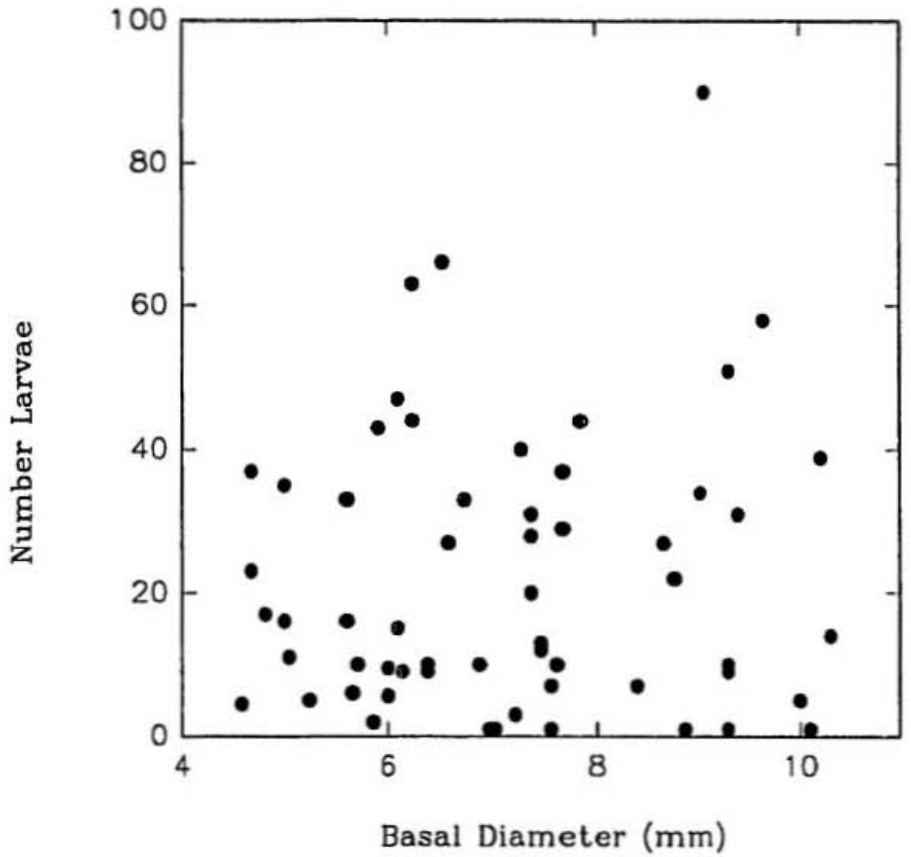


Figure 19: Relationship between number of overwintering Instar II larvae/branch and the basal diameter of the branch (n=61, r=0.36).

considerably lower than the number of first instar mines found on the same branches.

III.C.v: Population Changes:

The relative populations of birch casebearers on trees of the four treatment groups are indicated in Figure 20. In spring, 1991, larval populations were highest in severely damaged trees, next highest in lightly damaged trees; both mechanically damaged and control trees had no larvae present. Egg density on severely defoliated trees dropped below that of light and mechanically damaged trees, but remained higher than that on control trees. In August, 1991, there were more Instar II larvae on severely damaged than on lightly damaged trees. Numbers on severely damaged trees dropped in December, and dropped again to the lowest of the four treatment groups in March, 1992. Lightly-damaged trees had the most larvae during March. Percent feeding damage in spring, 1992 was highest in severely-damaged trees, next highest in lightly damaged trees, then control, and lowest in mechanically damaged trees, similar to the initial population pattern in June, 1991. The number of pupae in severely damaged trees was lower than those of the lightly damaged trees, yet they remained higher than the estimate on mechanically-damaged and control trees in July 1992.

Table 11: Number of Instar I mines (#/branch) and number Instar II larvae (#/branch) showing mean and standard deviation of three different aged leaves (young, medium and old) in 1992.

	Young leaves (# mines)	Medium aged leaves (# mines)	Old leaves (# mines)	Total number Instar I mines	Total number Instar II larvae
Mean:	0.091	3.364	2.864	6.318	0.773
St.Dev.:	0.294	3.632	3.342	5.149	1.020

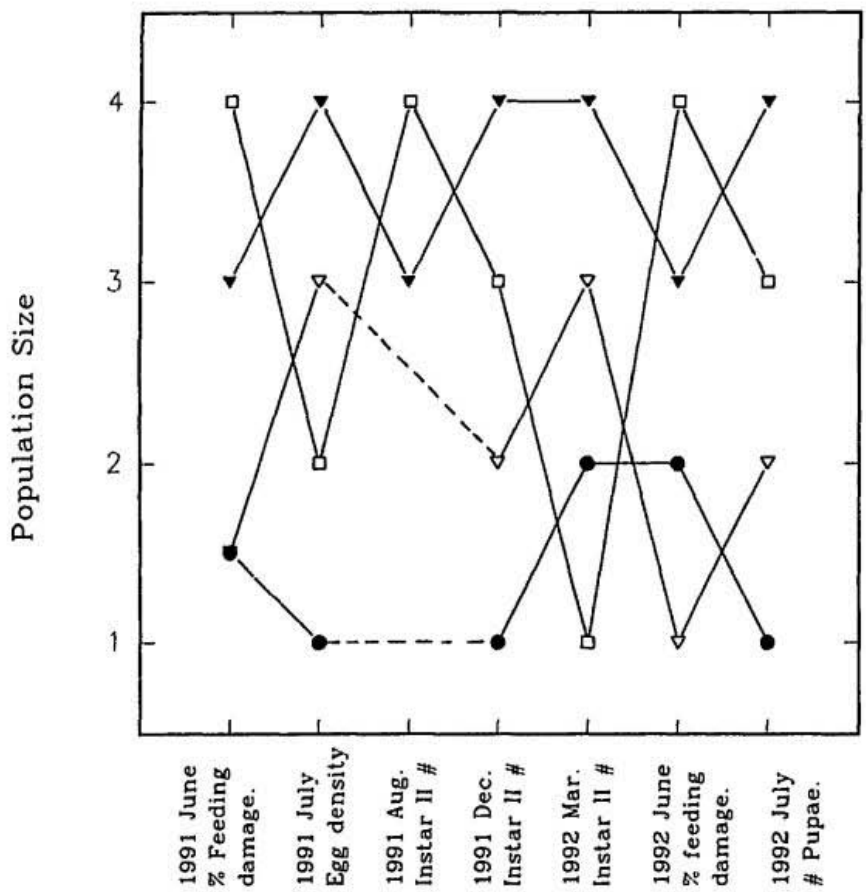


Figure 20: Relative size of birch casebearer populations between four treatment groups; severe (open squares), light (solid triangles), mechanical (open triangles), and control (solid circles) from spring 1991 to fall 1992.

III.D: Effects of Plant Changes on Larvae

III.D.i: Oviposition Tests:

Early trials (July 6 to July 30) resulted in moths emerging, but they were inactive and remained on the floor of the cage. No moths emerged in later trials (August 1 to 18). There were no eggs found on the leaves for any of the trials.

A total of 83 pupae were examined. Seventy-seven percent had been parasitized, 7% contained dead moths, and the remaining 16% contained pupal exuvium, indicating that the moths had emerged.

III.D:ii: Headcapsule Widths:

Headcapsule widths of Instar III larvae in both estimates in spring, 1992, showed no significant differences among treatment groups ($F_{(3,199)}=0.35, P>0.05$) and ($F_{(3,91)}=2.39, P>0.05$).

IV. Discussion

IV.A: Host Plant Development

IV.A.i: Nitrogen:

The seasonal variation in nitrogen levels corresponded to patterns described by Chapin (1980) (Figure 2). The history of birch casebearer infestation was thought to be the same for all twenty study trees in previous years. Therefore the significantly higher early season (July 10) 1991 leaf nitrogen levels of severe and control trees (Table 2) was not anticipated, although other factors also could be involved such as fertilizer contamination, or unseen bacterial or fungal infections.

Differences in nitrogen levels between treatment groups changed by mid season (Table 2, Figure 2). Leaves of severe and lightly damaged trees had higher nitrogen levels than leaves of the other two groups. Herbivores will deplete a plant of nitrogen reserves simply by consuming them; if some tissue is left, nitrogen is translocated from older leaves to younger, growing leaves, as a plant response to injury (Mattson, 1980). If more nitrogen than normal is transported

to younger leaves in a heavily defoliated tree, then levels of leaf nitrogen would seem higher in that tree. This might explain why the defoliated trees in this study (severe and light) had higher nitrogen levels than the undefoliated trees (mechanical and control) at mid season.

Levels of late season 1991 leaf nitrogen were higher in the undefoliated trees (mechanically damaged and control) than in the defoliated trees (severe and lightly damaged) (Table 2, Figure 2), although differences were not significant. If high levels of defoliation persisted from early season, leaf nitrogen levels would become depleted by herbivore consumption.

The significantly higher nitrogen levels in early 1992 compared to early 1991 (Table 2, Figure 2) may have occurred as a result of sampling. The sampling date in 1991 was July 10, whereas in 1992 it was June 24. Although chronological dates are not always indicative of plant developmental stages, leaves may have been fully expanded on July 10, 1991 but not fully expanded on June 24, 1992. Chapin et al (1980) reported that over a thirteen day period, the nitrogen content of birch leaves can change dramatically at the time of leaf flush. Therefore, small changes in sampling times from one year to the next could have a large effect on the nitrogen levels.

According to the definition of the delayed inducible response, any change exhibited by a tree due to herbivory

should be apparent in the season following damage to the tree (Haukioja, 1990). A delayed induced change of trees to previous season damage was seen in the order of increasing 1992 nitrogen levels among treatment groups. The nitrogen levels were inversely related to the extent of early season insect feeding damage to the trees in 1991 (Table 2, Figure 2). Defoliated trees (severe and light) had lowest mean leaf nitrogen levels, the mechanically damaged trees had higher mean nitrogen levels, and the undamaged trees (control) had highest mean nitrogen. It seems that birch casebearers had consumed the nitrogen in the defoliated trees, whereas there was no loss of tissue, and consequently nitrogen, in mechanically damaged and control trees. The induced change was caused by previous season damage but was a passive consequence of the damage rather than an active response to the damage by the tree. The end result of this passive change would be the same as from an active plant response, if it reduces the intensity of subsequent attack.

There is an inverse relationship between leaf nitrogen levels and phenolic content in birch (Haukioja et al, 1978, Tuomi et al, 1984). Thus, as leaf nitrogen levels decreased in the severely defoliated trees, the phenolic content likely increased. Phenolics are rather stable end products (Mattson, 1980), and once they are produced by the tree they remain for some time. Phenolics are carbon based and act as insect

deterrents by binding with nitrogen in the insect gut making it unavailable for use by the insect (Feeny, 1969). Since high phenolics are found to occur with low leaf nitrogen, then the passive defense of birch becomes more complex.

IV.A.ii: Phosphorus:

The 1991 seasonal decrease of leaf phosphorus levels was similar to and positively correlated with that of nitrogen (Figures 2 and 3). The seasonal decrease in phosphorus levels has also been shown to occur in leaves of beech, horse chestnut, and sycamore trees (Guha and Mitchell, 1966), and is considered the norm (Chapin, 1980). Guha and Mitchell (1966) suggested that almost the total supply of phosphorus for a tree is taken up early in the season, and thereafter phosphorus concentration decreases. Phosphorus does not accumulate in mature leaves, implying that it is mobilized and translocated to younger tissues (Guha and Mitchell, 1966).

Implications concerning herbivory would apply to both nitrogen and phosphorus since they positively correlated with one another (Figure 3). Leaf phosphorus depletion through insect consumption probably lowered the plant's reserves for the following season.

IV.A.iii: Leaf Nutrient Integration:

Differences in nitrogen and phosphorus levels among

treatment groups parallelled one another since they were positively correlated (Figure 3). This indicated that they were consumed similarly by the herbivore.

Both treatment and time of season in 1991 interacted significantly to affect leaf nitrogen and phosphorus levels. Unlike nitrogen, treatment had a significant effect on phosphorus levels. This suggests that if sampling continued into the 1992 season, nitrogen levels also would have been affected by treatment.

The increase in nitrogen and phosphorus levels from mid to late season for mechanical and control trees might have been a result of the sampling method. Samples in July 1991, consisted of younger leaves for severe trees, a mixture of young and old leaves for light trees, and a larger proportion of older leaves for mechanical and control trees. Because younger leaves contained higher nitrogen and phosphorus levels than older leaves, at mid season the late flushing leaves of severely and lightly damaged trees likely contained higher nutrient levels than older leaves of mechanical and control trees (Figure 2).

Position of the trees in the field may have contributed to variation in nutrient levels. Half the control trees were adjacent to a vegetable field which was fertilized each summer so that nitrogen and phosphorus enrichment from the field was possible. The severe, mechanically damaged and other half of

the control trees were intermixed and surrounded by alders and conifers. Alders, through their nitrogen fixing capability, have been shown to improve the foliar nitrogen and ring growth of nearby spruce trees (Hudson, 1985). The severe, mechanically damaged, and control trees were closer to the fertilized field than the lightly damaged trees. The lightly damaged trees were adjacent to a river and surrounded by small shrubs and grasses, and as a result could not receive excess nitrogen from the alders or the field.

IV.A.iv: Leaf Area:

Leaf area measurements did not provide strong evidence for an inducible change due to leaf damage. Kozlowski et al (1991) postulated that leaf size would be larger the following season as a response to damage. In contrast, Tuomi et al (1989) suggested that if nitrogen and phosphorus are depleted in a given year, leaf size should be smaller the following year. Kolodney-Hirsch and Harrison (1982) found that new leaves become larger following insect damage, due to an increase in cell size. It is not known if the large difference in mean leaf area among the four treatment groups in 1991 (Figure 4) was due to defoliation since defoliation histories of the trees were unknown.

Differences in mean leaf area among treatment groups from 1991 to 1992 (Table 8) may be explained partially in terms of

insect defoliation levels. Mean leaf areas of all groups, except that of the mechanically damaged, were larger in 1992 than 1991 (Figure 4). These larger leaves may in part be due to more nitrogen and phosphorus available in spring, 1992 (Tables 1 and 2) rather than a response to defoliation, since the larger leaf size of the control group was similar to that of the two insect infested groups.

Alternatively, the severe and lightly damaged trees may have responded to insect defoliation in 1992. Leaves of severe trees were largely consumed upon bud opening in 1991 (Figure 4). Severely damaged trees had significantly smaller leaves in 1992 than undamaged or lightly damaged trees as a result of insect feeding (Table 8). Larger leaves of severely and lightly damaged trees in 1992 (Figure 4) and those with insect feeding in 1991, may have been a result of a delayed compensation of the tree by increasing leaf size. Since there was less feeding damage in 1992 than 1991 in both severely and lightly defoliated trees (Figure 14), more nitrogen and phosphorus were available for leaf growth in 1992. The mechanically damaged trees may not have shown a larger leaf size for several reasons; the damage consisted of tearing rather than loss of tissue and nutrients; there was no fertilizer contamination from an adjacent field; there was no insect defoliation; or they may have already reached maximum size by the time of sampling in 1991.

Although there was no interaction effect between quadrant and treatment on 1991 leaf areas, each independently had a significant effect on leaf size. Larger leaves in lower south quadrants (Figure 5) may have been due to shading. As a portion of the light is intercepted by the upper canopy, an increase in the photosynthetic area of the lower leaves would increase their ability to absorb the available light.

IV.A.v: Bud Development and Leaf Senescence:

Changes in a subsequent season within a tree to insect damage may involve shorter shoots and fewer buds (Edwards et al, 1992), late leaf flush in the following year, and smaller leaves on damaged branches than on undamaged branches (Tuomi et al, 1989). This study confirmed that shoots were shortest and buds fewest on severely damaged trees, and were longest and most numerous on mechanically and lightly damaged trees (Figure 6). Severely damaged trees may have been depleted of their reserves to such a degree that shoot and bud development were suppressed, and the ability to compensate for losses was eliminated. This is considered a passive plant change as a consequence of, rather than as an active response to, insect feeding damage in the previous year. There may have been some compensation for insect damage on lightly damaged trees because loss of leaf tissue was not as great as in severely damaged trees. Mechanically damaged trees lost no tissue but

rather were subjected to tissue tearing. Shoots were longer and number of buds were fewer in mechanically and lightly damaged trees than in controls. This suggests that mechanically and lightly damaged trees had compensated for their loss whereas severely damaged trees had not. McNaughton (1983) reviewed compensatory plant growth as a response to herbivory and concluded that moderate herbivory may actually increase plant fitness.

Delayed bud break in the following season could have a negative impact on overwintering herbivores waiting for the first leaf flush in the spring. If bud break is delayed in birch, then the overwintering Instar II larvae may use all or a major portion of their stored reserves before leaves become available, and starvation may ensue. Early season artificial defoliations induces a significant delay in budbreak the following year (Tuomi et al, 1989). Although this change is passive, it can have the same result as an active response in that the tree can be rendered less suitable for herbivores. The change in development is probably a direct result of a depletion of resources from the previous year.

Slower development of buds of the severely damaged trees in the second season (Figure 8) indicated a delayed induced change of the birch tree to the severe insect damage of the previous season. Hunter (1992) discovered that severely infested oak trees which leaf out early, support higher

caterpillar populations and suffer higher levels of defoliation than those which leaf out late. Late budburst had a negative impact on the insects waiting to feed on those leaves.

The early leaf senescence in severely damaged trees of this study may have been a result of low nutrient reserves in both 1991 and 1992, as insect feeding damage was relatively high in both years (Figure 14). A delay in the onset of senescence may occur following partial defoliation (Belsky, 1986). Belsky (1986) suggested that the decrease in leaf area as a result of defoliation reduced competition among roots for nutrients, ard this reduction in nutrient loss helped to delay senescence.

IV.B: Water Relations

IV.B.i: Water Relations of Host Plant:

Three phases have been recognized in the seasonal dry weight of leaves (Ballard and Petrie, 1936 In Williams, 1955). The first is referred to as 'adolescence', which is the initial growth period. The second phase, 'maturity', is a period of constant weight after cessation of growth, and the third, 'senescence', is a period of decline in weight and internal disorganization. In this study the adolescence phase occurred until about July 10, leaf maturity occurre om July 10 to about August 16, and senescence occurred between August

16 and September 27 (Figures 10 and 11).

An increase in dry weight may involve an increase in cellulose, lignin, starch or secondary compounds. Since water content, and nitrogen and phosphorus levels decreased throughout the season (Figure 12), the increase in fresh weight throughout the season was attributed to an increase in dry matter consisting of carbohydrate compounds. Feeny (1970) attributed increasing toughness of oak leaves to deposition of cellulose, hemicelluloses, pectins, and other materials into the cell walls.

It has been suggested that some physiological activities such as leaf senescence are better correlated with changes in water content than water potential (Kozlowski et al, 1991). However, it has also been argued that water movement is controlled by differences in water potential (Kozlowski et al, 1991).

Water stress can cause premature senescence (Kozlowski et al, 1991). Senescence involves complex interactions of hormones and nutritional balance. The decrease in water during senescence would reduce the supply of carbohydrates and nitrogen to leaves, which occurs at the same time as a drop in cytokinins and an increase in ethylene, promoting leaf senescence (Kozlowski et al, 1991). Since a water deficit is an indication of leaf senescence before the leaves actually turn yellow, then an increase in xylem pressure was used in

this study to signify the onset of leaf senescence. Senescence of the birch leaves in this study began on August 11 (Figure 12), coinciding with a seasonal drop in water content. The leaves exhibited color changes on September 10.

IV.B.ii: Young and Old Leaves:

The rapid increase in weights of young leaves until September 10 suggests nutrient translocation from older to younger leaves. However, specific fresh weights of young leaves decreased, as the specific dry weights increased (Figure 11), indicating water content decreased with the onset of senescence (Figure 12). This may have been an indication that the abscission zone was forming, reducing the amount of water entering the leaf. The increase in specific dry weights suggested that carbohydrates had not yet left the leaf even though senescence seemed to be occurring. Cells in the abscission zone become more lignified than others around them, and they compress the vascular tissue traversing the zone (Addicott, 1982).

In contrast, when specific fresh weights and water content of old leaves decreased, specific dry weights remained constant (Figures 11 and 12). Old leaves appeared to be further along in the senescence process late in the season than young leaves, since it appeared many of their carbohydrates had already been removed.

Xylem pressures at the end of the season were similar in old and young leaves, being slightly higher in the older leaves than in the younger leaves (Figure 13). Older leaves apparently senesced first with their nutrients being translocated from them for winter storage.

IV.B.iii: Water Relations and Insect Larvae:

IV.B.iii: (a) Direct Effects:

Survival of early-instar larvae that enter the leaf for shelter and food may be affected by leaf water content directly by too little or too much water. The lower leaf water content on July 31 (egg hatch) (Figure 12) provided less moisture to the larvae. Shortly after egg hatch, water potential began to fluctuate (Figure 13) as turgor pressure inside the leaf increased. Because Instar I larvae feed and live entirely within a birch leaf, moisture loss from the larvae is reduced to a minimum. Just prior to and during senescence (August 16 to September 27) (Figure 13) larvae molt to Instar II. These larvae live external to the leaf but inside a case and are therefore able to maintain humid conditions within their cases, but are still able to move from leaf to leaf. If water is too low or too high in one leaf they can move to another leaf.

IV.B.iii: (b) Indirect Effects:

Variation in water content indirectly affects availability of nutrients (Scriber, 1977), concentration of available nutrients (Mattson, 1980), and the timing of the onset of leaf senescence (Kozlowski et al, 1991), all of which may affect the survival of leafmining larvae.

Incorporation of carbohydrates into cell walls in birch leaves reduces the nutritional and digestibility value of leaves in the latter half of the season when the first and second instars are active. Scriber (1977), in experiments with low leaf water content, showed that species of Lepidoptera were unable to use the nitrogen present, and this caused slow larval growth. Since insect growth rate is dependent on nitrogen accumulation rate, changes in nitrogen assimilation brought about by changes in dietary moisture are especially critical to insect development (Mattson, 1980).

Eggs were laid on medium and old leaves and these were the leaves on which the Instar I mines occurred. Egg hatch coincided with the second leaf flush at which time the first of the youngest leaves had just fully expanded. On July 17 a drop in water potential and water content occurred (Figures 12 and 13), which might have indicated the onset of the second leaf flush. If soil nutrient supply is insufficient, nutrients required for the continued growth of young leaves

come from the older leaves (Chapin, 1980). If the second leaf flush in birch in this study drew nutrients from the older leaves where the eggs were laid, then the re-mobilized nutrients out of the leaf would be available for the hatchlings mining that leaf. At the time of year when Instar I and II larvae are active, nitrogen, water content, and leaf palatability are relatively high (Haukioja et al, 1978), and leaf toughness and phenolics are relatively low (Schultz et al, 1982). Prior to and during senescence, nitrogen and other nutrients are not only prevented from entering the leaves, but also are mobilized and translocated out of the leaves and into the twigs for winter storage (Kozlowski et al, 1991). If the timing of the second instars occurs during this critical stage of high nutrient supply, then their chances of survival would be greater. Instar II larvae are able, if necessary, to move from leaf to leaf in search of better quality food.

Maturing Instar III and IV larvae feed on early season leaves and buds high in nitrogen, phosphorus, and moisture, and presumably low in phenolics and toughness. If younger instars require for growth and development, a diet higher in nutrients and moisture than the later instars, one would expect late instars to emerge in late summer, and early instars in early summer. However, according to White (1974), it is the early instars which are more vulnerable to changes in leaf nitrogen content. In this study the highest degree of

change occurred early in the season (Figure 2), and thereafter the change was not as pronounced.

Larval stages of two leafmining birch sawflies (Fenusa pusilla (Lepeletier) and Messa nana Klug) co-occur with birch casebearer and are much shorter in duration than that of birch casebearer instars I and II larvae (DeClerek and Shorthouse, 1985). Mines of these sawflies appeared August 16 (Figure 13), just prior to Instar II birch casebearer larvae, and therefore appear to be using similar adaptations for survival.

Fenusa pusilla feeds in late season on both palisade and spongy mesophyll of very young birch leaves, presumably high in nitrogen and moisture. M. nana is a late season feeder on the upper palisade of mature leaves (DeClerck and Shorthouse, 1985). There is more chlorophyll in the upper palisade and the cells are more tightly compacted than in the lower mesophyll. More upper mesophyll is consumed by the sawfly larva than lower mesophyll. Instar I and II birch casebearer larvae feed on both upper and lower mesophyll layers.

Gaston et al (1992) suggested that internal feeders tend to be more specialized in their habits as they choose cells to consume, than external feeders. Internal feeders would be more successful on heavily defended plants than external feeders, because they can circumvent physical and chemical defenses by selective feeding (Gaston et al, 1992). Whole holly leaves are low in nitrogen and water, but the palisade

mesophyll is chlorophyllous, rich in protein, and contains abundant water, although the saponin content is 10-fold higher than in the leaf as a whole. Thus the holly miner, which feeds on the palisade mesophyll, has adapted to a food source rich in nutrients but also high in allelochemicals (Kimmerer and Potter, 1987). Similarly, if Instar I birch casebearer larvae have adapted to high late season phenolic content (Haukioja et al, 1978), then they also have a food source rich in nutrients. For another study, sexual maturation in desert locusts was delayed when they were fed on senescent vegetation, due to a shortage of gibberellins which are present in the young leaves (Ellis, Carlisle, and Osborne, 1965). The meristematic leaf tissue in birch buds would also be high in gibberellins since this is the hormone that stimulates plant growth. Early season birch casebearer Instar III and IV larvae consume these nutrient and moisture rich leaves which would increase fecundity of the females.

IV.C.: Population Estimates

Birch casebearer populations on the four treatment groups oscillated over the two year study period, but for the most part the heavier insect infestations remained heavy, and the lighter infestations remained lighter (Figure 20). Moths seemed to remain within the vicinity of the tree in which they pupated.

IV.C.i: Feeding Damage by Instar III and IV Larvae:

There was no large scale dispersal of moths among study trees since the pattern of feeding damage between insect-damaged treatment groups in spring 1992 was similar to that of 1991 (Table 8). For the most part, the severely damaged trees remained severely damaged, and the other three groups became lightly damaged (Figure 14) as moths slowly dispursed among them.

IV.C.ii: Egg Density:

Since there was no interaction effect of canopy level and treatment group on egg density, each factor was treated separately. Differences in egg density on leaves among the treatment groups (Figure 17) might have been due to positional effects. Half the control trees, which initially had no larvae, were located further away from the severely damaged trees than the mechanically damaged and the other half of the control trees. Moths would have had to travel up to forty meters of open space to oviposit on the trees further away. The severely damaged trees in the mid 1991 season contained very few leaves, and many of these were brown and not ideal for oviposition. The mechanically damaged trees were adjacent to the severe and the other half of the control trees, and therefore provided green leaf oviposition sites for moths dispursing from severe trees. Because the lightly damaged

trees were not as densely inhabited as the severe trees, they provided more mining area for hatchlings. This pattern of egg laying suggested that the moths probably only moved if there was not sufficient space and food where they were, otherwise they remained near the same tree they pupated on, and oviposited on high quality leaves within that tree.

The positive correlation between 1991 mid season nitrogen levels and number of eggs per leaf (Figure 16) suggested that female birch casebearer moths were able to distinguish between high and low nitrogen levels, and chose the better quality leaves for oviposition. The same correlation was not found with phosphorus, therefore high nitrogen could be a deciding factor. Even though this suggests that moths choose trees whose leaves on average had high nitrogen on which to lay eggs, they may also choose among leaves within the same tree, or adjacent trees. In another study, female pine beauty moths laid more eggs on previously undefoliated lodgepole pine than on those which had been defoliated the year before (Leather et al, 1987). This oviposition preference was attributed to changes in oleoresin levels within the needles.

IV.C.iii: Overwintering Larvae:

Lightly damaged trees had higher numbers of eggs as well as overwintering larvae. Although differences in larval counts among treatment groups were not significant, March larval

counts were significantly lower than the December counts (Figure 18). The lightly damaged trees had the highest number of larvae at both times of the year.

Severe, mechanical, and control treatment groups were closer to a stand of coniferous trees frequented by birds than the lightly damaged trees. Many birch casebearer larvae were probably preyed upon by birds. The high density of larvae on mechanically damaged trees was easily accessed by birds. Harsh snow and ice storms would also add to larval mortality.

IV.C.iv: Population Changes:

IV.C.iv.(a) Effects of Artificial Damage:

This study showed that the mechanically damaged trees had the second highest number of eggs and overwintering larvae, but the lowest amount of feeding damage in 1992 (Figure 20). This probably occurred because mechanically damaged trees had the largest leaf areas in both years. Proportionally, feeding area is not as great on large leaves as it would be on small leaves if the amount of feeding was the same on both. Also, percentage of leaf area missing from mature leaves may not provide an accurate estimate of the actual leaf area consumed by larvae due to the distortion of the young growing leaves as they are consumed (Landsberg and Ohmart, 1989). Methodological problems, such as these need to be overcome in order to standardize leaf areas. Nevertheless, larvae seemed

to be unaffected by mechanical damage in this study.

IV.C.iv.(b) Leaf Nutrients, Egg Density, and Feeding Damage.

Tuomi et al (1984) reported that as leaf nitrogen levels fall, phenolic content rises. Even though insect damage was high in severe and lightly damaged trees at the beginning of 1991, in mid season 1991 the nitrogen levels of these trees were high relative to that of the other groups, indicating that phenolic content was low. The majority of eggs were laid on lightly damaged, second highest on mechanically damaged, and with the third highest density on severely damaged trees. Insect damage on severely defoliated trees in 1992 remained higher than that on mechanical and control trees (Figure 20), but nitrogen was low (Figure 2). This appears disadvantageous to the third instars, in that those on severely damaged trees would need to consume a large portion of leaf tissue to obtain sufficient nitrogen for growth. Although leaves of severely defoliated trees were larger in 1992 than 1991, they remained smaller than those of any of the other three groups. Comparatively, the smaller leaf size, and larger amount of tissue consumed by Instar III and IV larvae on severely defoliated trees in 1992, would account for the apparent larger amount of feeding damage present. Although casebearer populations on severely damaged trees were lower than those of other trees, fewer and smaller leaves on the severely damaged

trees resulted in more apparent damage.

IV.C.iv.(c) Summary of Population Changes:

Overall, the two year study revealed that birch casebearer populations tend to remain localized. If low nutrition (and/or high phenolic content) is sufficient to deter other insect species, it had no apparent effect on the birch casebearer. Instead it seems that space allocation, in conjunction with the actions of predators, were the controlling factors for the populations of Instars III and IV casebearers. Faeth (1986) found that leafminers avoided damaged leaves, suggesting that there was no discrimination between damaged and undamaged trees, but rather leafminers selected leaves within trees. Feeding damage of early season leaf-chewers produced higher levels of tannins and lower protein content in damaged leaves within trees, but it had no effect on between tree chemistry differences. Similarly, Bergelson et al (1986) found that C. serratella, the birch casebearer, would move small distances away from leaf damage, often remaining on the same leaf or moving to an adjacent leaf. Tuomi et al (1989) reported that low nitrogen and high phenol contents, a consequence of defoliation from the previous year, were significantly higher in defoliated branches than in control branches of the same tree. It seems that even when birch casebearer larvae avoided damaged leaves,

they did not always avoid trees containing the damaged leaves.

IV.D: Effects of Plant Changes on Larvae

IV.D.i: Headcapsule Widths:

Headcapsule widths of Instar III and IV larvae in spring 1992, measured at two different sampling times, did not differ significantly between treatment groups. Thus it appeared that any induced changes of white birch had no measurable effect on larval growth.

Bergelson et al (1986) found that C. serratella larvae reared on damaged trees took significantly longer to develop (three days longer) than those on undamaged trees, though there was no increase in mortality. Similarly, growth rates and pupal weights of Oporinia (=Epirrita) autumnata (Bkh.), the autumnal moth, were reduced in those insects grown on damaged leaves compared to those on undamaged leaves in both short and long-term studies (Haukioja and Niemela, 1977).

Both mechanical and insect damage to leaves of mountain birch reduced the growth of E. autumnata (Bkh.) in the following year, though in similar studies on willow there was no difference (Neuvonen et al, 1987). Aggregated O. autumnata larvae grew better than solitary ones on birch leaves with strong, long-term induced defenses elicited, whereas solitary larvae grew better than crowded ones on high quality birch leaves (Haukioja, 1980). This was explained as a 'density

induced adaptation' of the moth to the defensive tactics of the host tree. Haukioja (1980) stated genetic changes in herbivore populations during cycles are almost inevitable because selection pressures must differ at different phases of the cycle due to varying levels of plant defenses. If larvae are reared on leaves with high levels of plant defensive agents, they then will become genetically adapted to those levels. Leaves with lower or higher levels of such plant defenses may reduce insect growth.

V. Conclusion

Host plant induced changes due to damage were evident in birch as relatively low nitrogen levels, short long-shoots, fewer buds, and delayed budbreak the following season. These host plant changes seemed to have no effect on the birch casebearer. This supports Fowler and MacGarvin's (1986) finding that C. serratella had very little sensitivity to damage-induced changes in birch foliage. Many phenolics have long been recognized as fungicidal and bactericidal agents (Friend, 1980), and therefore may not be as powerful deterrents against some insects, such as birch casebearer, as others. This study showed no evidence for damage induced responses by the host plant.

The large and fast-growing Instar III and IV larvae consume the early season, high nitrogen birch leaves. This might increase fecundity in the female moths which emerge mid season.

The seasonal timing of Instar I and II larvae coincided with lower leaf water content and the re-mobilization of leaf nutrients. This suggests two hypotheses. First, low leaf water content is necessary for larval survival in that if leaf

water levels are too high the larvae may drown. Second, low leaf water levels indicate that nutrients are being re-mobilized either to newly emerging leaves, or to twigs and roots for winter storage. Moderate water stress, created by initial stages of senescence, increases leaf nitrogen, making it available for insect consumption. As well, re-mobilization of nutrients would also make them available to the insect.

Further study of the host tree-birch casebearer herbivore system should involve more localized and well-defined experiments, such as within tree experiments using single leaves, or groups of related leaves as treatment groups. Laboratory bioassays, such as choice tests for the ovipositing female moth, would also be an asset.

VI. Summary

1). The effects of damage-induced and developmental changes of white birch on birch casebearer larvae was studied in Goulds, Newfoundland in 1991 and 1992.

2). Four groups of five white birch trees each were selected and treated so as to be severely damaged by insects, lightly damaged by insects, mechanically damaged by puncturing the leaf lamina with no insects present, and control trees with neither type of damage present.

3). Rapid and delayed damage-induced changes between treatment groups were measured and related to the activity and growth of birch casebearer. Leaf water contents and xylem pressures were used to indicate leaf developmental processes.

4). There was a significant interaction effect of treatment and time of season in 1991 on leaf nitrogen levels. Time of season had a larger effect on nitrogen than treatment. Leaf nitrogen and phosphorus levels were highest in spring then dropped, and remained low throughout the season.

5). Nitrogen and phosphorus levels in early season 1992 were significantly higher than early season 1991 levels. Differences in sampling dates between years may account for

this variation.

6). A delayed damage-induced change of the tree was evident in the differences between early season nitrogen levels of 1991 and 1992 among treatment groups. The higher nitrogen in the undefoliated trees than in the defoliated trees suggested that the degree of damage to the leaves may have affected the amount of stored nitrogen available for the following season. These changes were viewed as physiological consequences of defoliation, or 'a by-product of mechanisms which rearrange the plant carbon/nutrient balance in response to nutrient stress caused by defoliation' (Tuomi et al, 1984).

7). Leaf area measurements did not provide strong evidence for an inducible change due to leaf damage.

8). Long-shoot length and number of buds were lower on severely damaged trees than on trees of other treatment groups in 1992. This was considered a passive change in the tree as nutrients were depleted by insect feeding the previous year eliminating the tree's ability to compensate for losses.

9). Budbreak in 1992 was delayed in severely damaged trees. This might have been a response to damage, but was likely a passive consequence of nutrient depletion. Early senescence of leaves on severely damaged trees also may have been a result of low reserves.

10). Since water content of leaves decreased over the season, the increase in fresh weight was attributed to the

increase in dry weight. Since nitrogen and phosphorus decreased, dry weight presumably consisted of carbohydrate compounds which added bulk to the insect's food.

11). Egg hatch coincided with second leaf flush. Since eggs were laid on old leaves, it was postulated that they took advantage of the nutrients being mobilized out of the old leaves moving into young leaves. It was also suggested that lower leaf water levels prevented larval mortality from drowning.

12). Similarly, Instar II larvae consumed tissue rich in mobilizing nutrients as senescence occurred.

13). The late season increase in specific dry weights of young leaves, as they were decreasing in older leaves suggested that carbohydrates had not left the leaves even though senescence had begun.

14). The similarity of feeding damage between treatment groups in 1992 with that in 1991 suggested that female moths did not move far from the site of pupation.

15). Since leaves on severely damaged trees were small and brown from intense insect feeding in spring 1991, low egg density may have been due to insufficient oviposition leaf space for the severely damaged trees.

16). Positive correlation between nitrogen levels and egg density suggested that female moths might be able to distinguish between high and low nitrogen levels, though this

might easily occur within the same tree. It seems that large, extensively branching individual plants, as with white birch, are actually colonies of many heritable genotypes, or genetic mosaics (Gill, 1986).

17). Although differences in overwintering larval counts among treatment groups were not significant, March larval counts were significantly lower than the December estimates.

18). Since headcapsule widths of spring, 1992, Instar II larvae did not differ significantly between treatment groups, it appeared that induced changes of white birch had no measurable effect on larval growth.

19). Birch casebearer populations on the four treatment groups oscillated over the two year study period, but for the most part the heavier insect infestations remained on the same group of trees.

VII. References

Addicott, F. T. 1982. Abscission. University of California Press, Berkeley. 369 pp.

Baldwin, I. T. 1990. Herbivory simulations in ecological research. TREE 5(3): 91-93.

Bergelson, J. M. and Lawton, J. H. 1988. Does foliage damage influence predation on the insect herbivores of birch? Ecology 69(2):434-445.

Bergelson, J., Fowler, S., and Hartley, S. 1986. The effects of foliage damage on casebearing moth larvae, Coleophora serratella, feeding on birch. Ecol. Entomol. 11:241-250.

Belsky, A. J. 1986. Does herbivory benefit plants? A review of the evidence. Am. Nat. 127:870-892.

Bradstreet, R. B. 1965. The Kjeldahl method for organic nitrogen. New York. Academic Press. 239 pp.

Bryant, J. P., Chapin, F. S. III, Reichardt, P. B., and Clausen, T. P. 1987. Response of winter Chemical defense in Alaska paper birch and green alder to manipulation of plant carbon/nutrient balance. Oecologia. 72:510-514.

Bryant, J. P., Heitkonig, I., Kuropat, P., and Owen-Smith, N. 1991. Effects of severe defoliation on the long-term resistance to insect attack and on leaf chemistry in six woody species of the southern African savanna. Am. Nat. 137:50-63.

Chapin III, F. S. 1980. The mineral nutrition of wild plants. Annu. Rev. Ecol. Syst. 11:233-260.

Chapin III, F. S., Johnson, D. A., and McKendrick, J. D. 1980. Seasonal movement of nutrients in plants of differing growth form in an Alaskan tundra ecosystem: Implications for herbivory. J. Ecol. 68:189-209.

Cochran, S. G. 1970. The birch casebearer in Newfoundland. Forest Research Laboratory, St. John's, Newfoundland. Internal Report N-32. Canadian Forestry Service, Department of Fisheries and Forestry. August, 1970.

Coley, P. D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecol. Monogr. 53:209-233.

Coshan, P. F. 1974. The biology of Coleophora serratella (L.) (Lepidoptera: Coleophoridae). Trans. R. Ent. Soc. Lond. 126(2):169-188

DeClerck, R. A. and Shorthouse, J. D. 1985. Tissue preference and damage by Fenusa pusilla and Messa nana (Hymenoptera: Tenthredinidae), leafmining sawflies on white birch (Betula papyrifera). Can. Entomol. 117:351-362.

Edwards, P. J., Wratten, S. D., and Parker, E. A. 1992. The ecological significance of rapid wound-induced changes in plants: insect grazing and plant competition. Oecologia. 91:266-272.

Ellis, P. E., Carlisle, D. B., and Osborne, D. J. 1965. Desert locusts: Sexual maturation delayed by feeding on senescent vegetation. Science. 149:546-547.

Faeth, S. A. 1986. Indirect interactions between temporally separated herbivores mediated by the host plant. Ecol. 67:479-494.

Feeny, P. P. 1969. Inhibitory effect of oak leaf tannins on the hydrolysis of proteins by trypsin. Phytochemistry. 8:2119-2126.

Feeny, P. P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecol. 51:565-581.

Fowler, S. V. and Lawton, J. H. 1985. Rapidly induced defenses and talking trees: The devil's advocate position. Am. Nat. 126(2):181-195

Fowler, S. V. and MacGarvin, M. 1986. The effects of leaf damage on the performance of insect herbivores on birch, Betula pubescens. J. Anim. Ecol. 55:565-573.

Friend, J. 1980. Plant phenolics, lignification and plant disease. Progress in Phytochemistry. 7:197-262.

Gaston, K. J., Reavey, D., and Valladares, G. R. 1992. Intimacy and fidelity: Internal and external feeding by the British microlepidoptera. Ecol. Entomol. 17:86-88.

Gibberd, R., Edwards, P. J., and Wratten, S. D. 1988. Wound-induced changes in the acceptability of tree-foliage to Lepidoptera: within leaf effects. Oikos. 51:43-47.

Gill, D. E. 1986. Individual plants as genetic mosaics: Ecological organisms versus evolutionary individuals. pp. 321-344 In Plant Ecology (M. J. Crawley, Editor). Blackwell Scientific Publications, U. S. A.

Guha, M. M. and Mitchell, R. L. 1966. The trace and major element composition of the leaves of some deciduous trees II. Seasonal changes. Plant Soil. 24(1):90-112.

Hartley, S. E. and Lawton, J. H. 1987. Effects of different types of damage on the chemistry of birch foliage, and the responses of birch feeding insects. Oecologia. 74:432-437

Haukioja, E. 1980. On the role of plant defenses in the fluctuations of herbivore populations. Oikos. 35:202-213.

Haukioja, E. 1982. Inducible defenses of white birch to a geometrid defoliator, Epirrita autumnata. Proc. 5th Int. Symp. Insect-Plant Relationships, Wageningen, 1982. Pudoc, Wageningen, 1982. pp. 199-203.

Haukioja, E. 1990. Induction of defenses in trees. Annu. Rev. Entomol. 36:25-42.

Haukioja, E. and Hakala, T. 1975. Herbivore cycles and periodic outbreaks. Formulation of a general hypothesis. Rep. Kevo Subarctic Res. Stat. 12:1-9.

Haukioja, E. and Niemela, P. 1977. Retarded growth of a geometrid larva after mechanical damage to leaves of its host tree. Ann. Zool. Fennici. 14:48-52.

Haukioja, E., Niemela, P., Iso-Iivari, L., Ojala, H., and Aro, E-M. 1978. Birch leaves as a resource for herbivores. I. Variation in the suitability of leaves. Rep. Kevo Subarctic Res. Stat. 14:5-12.

Haukioja, E., Suomela, J., and Neuvonen, S. 1985. Long-term inducible resistance in birch foliage; triggering cues and efficacy on a defoliator. Oecologia. 65:363-369.

Haukioja, E., Ruohomaki, K., Suomela, J., and Vuorisalo, T. 1991. Nutritional quality as a defense against herbivores. Forest Ecol. Manage. 39:237-245.

Hudson, A. J. 1985. The influence of Alnus crispa (Ait.) Pursh on the growth, nutrition, and survival of Picea mariana (Mitt.) B. S. P. and Picea sitchensis (Bong.) Carr. in plantations near Mobile, Newfoundland. Honours Dissertation, Department of Biology, Memorial University of Newfoundland, Newfoundland. 44 pp.

Kimmerer, T. W. and Potter, D. A. 1987. Nutritional quality of specific leaf tissues and selective feeding by a specialist leafminer. Oecologia. 71:548-551.

Kolodney-Hirsch, D. M. and Harrison, F. P. 1982. Comparative damage and leaf area consumption by the tobacco budworm and corn earworm on Maryland tobacco. J. Econ. Entomol. 75:168-172.

Kozlowski, T. T., Kramer, P. J., and Pallardy, S. G. 1991. The Physiological Ecology of Woody Plants. Academic Press, Inc. London. 657 pp.

Landsberg, J. and Ohmart, C. 1989. Levels of insect defoliation in forests: Patterns and concepts. TREE.4(4):96-100.

Leather, S. R., Watt, A. D., and Forrest, G. I. 1987. Insect-induced chemical changes in young lodgepole pine (Pinus contorta): the effect of previous defoliation on oviposition, growth and survival of the pine beauty moth, Panolis flammea. Ecol. Entomol. 12:275-281.

Levin, D. A. 1976. The chemical defenses of plants to pathogens and herbivores. Ann. Rev. Ecol. Syst. 7:121-159.

MacDonald, A. D. and Mothersill, D. H. 1983. Shoot development in Betula papyrifera. I. Short-shoot organogenisis. Can. J. Bot. 61:3049-3065.

Mattson, W. J. Jr. 1980. Herbivory in relation to plant nitrogen content. Annu. Rev. Ecol. Syst. 11:119-161.

McNaughton, S. J. 1983. Compensatory plant growth as a response to herbivory. Oikos. 40:329-336.

Myers, J. H. and Williams, K. S. 1987. Lack of short or long-term inducible defenses in the red alder - western tent caterpillar system. Oikos. 48:73-78.

Neuvonen, S., Haukioja, E., and Molarius, A. 1987. Delayed inducible resistance against a leaf-chewing insect in four deciduous tree species. Oecologia. 74:363-369.

Noggle, G. R. and Fritz, G. J. 1983. Introductory Plant Physiology. Second edition. Prentice-Hall, Inc. New Jersey. 627 pp.

Nostrand, R. S. van. 1976. Management for maintenance of the fir- birch forest. Pp. 39-42. In B. J. Garland. Quality inventory white birch Central Newfoundland. Department of Forestry and Agriculture. Forest Inventory Division. Information Report. F1-No. 4. July, 1976.

Perala, D. A. and Alm, A. A. 1990. Reproductive ecology of birch: A review. Forest Ecol. Manage. 32:1-38.

Plaisted, P. H. 1958. Some biochemical changes during development and aging of Acer platanoides L. leaves. Contr. Boyce Thompson Inst. 19(3):245-254.

Raske, A. G. and Bryant, D. G. 1977b. Relation of birch casebearer (Lepidoptera: Coleophoridae) numbers to percent defoliation of white birch. Can. Entomol. 109:1307-1312.

Ruohomaki, K., Hanhimaki, S., Haukioja, E. Iso-Iivari, L., Neuvonen, S., Niemela, P., and Suomela, J. 1992. Variability in the efficacy of delayed inducible resistance in mountain birch.

Scriber, J. M. 1977. Limiting effects of low leaf-water content on the nitrogen utilization, energy budget, and larval growth of Hyalophora cecropia (Lepidoptera: Saturniidae). Oecologia. 28:269-287.

Schultz, J. C. and Baldwin, I. T. 1982. Oak leaf quality declines in response to defoliation by gypsy moth larvae. Science. 17:149-151.

Schultz, J. C., Nothnagle, P. J., and Baldwin, I. T. 1982. Seasonal and individual variation in leaf quality of two northern hardwood tree species. Amer. J. Bot. 69:753-759.

Senn, J., Hanhimaki, S. and Haukioja, E. 1992. Among-tree variation in leaf phenology and morphology and its correlation with insect performance in the mountain birch. Oikos. 63:215-222.

Thomson, W. T. 1979-1980. Agricultural Chemicals; Book 1. Insecticides, Acaricides and Ovicides. Thomson Publications, California. pp. 169-170.

Tuomi, J., Niemela, P., Haukioja, E., Siren, S., and Neuvonen, S. 1984. Nutrient stress: an explanation for plant anti-herbivore responses to defoliation. Oecologia. 61:208-210.

Tuomi, J., Niemela, P., Jussila,I., Vuorisalo, T, and Jormalainen, V. 1989. Delayed budbreak: a defensive response of mountain birch to early season defoliation? Oikos. 54:87-91.

White, T. C. R. 1974. A hypothesis to explain outbreaks of looper caterpillars, with special reference to populations of Selidosema suavis in a plantation of Pinus radiata in New Zealand. Oecologia. 16:279-301.

White, T. C. R. 1976. Weather, food, and plagues of locusts. Oecologia. 22:119-134.

Williams, R. F. 1955. Redistribution of mineral elements during development. Annu. Rev. Plant Physiol. 6:25-42.

Wratten, S. D., Edwards, P. J. and Dunn, I. 1984. Wound-Induced changes in the palatability of Betula pubescens and B. pendula. Oecologia. 61:372-375.